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The Canadian Oyster

Jos. Stafford

Commission of Conservation
Canada

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Commission of Conservation
CANADA

COMMITTEE ON FISHERIES, GAME AND FUR-BEARING ANIMALS

THE

CANADIAN OYSTER

Its Development, Environment and Culture

By

JOS. STAFFORD, M.A., Ph.D.

Ottawa:
The Mortimer Co., Ltd.
1913

Committee on Fisheries, Game and Fur-Bearing Animals

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May it Please Your Royal Highness:

The undersigned has the honour to lay before Your Royal Highness a report on the Canadian Oyster, its Development, Environment and Culture , by Joseph Stafford, M.A., Ph.D.

Respectfully submitted

CLIFFORD SIFTON

Chairman

Ottawa, Oct. 4, 1913

OTTAWA, Oct. 3, 1913

Sir:

I have the honour to transmit herewith a report on the Canadian Oyster, its Development, Environment and Culture, by Dr. Joseph Stafford.

Your obedient servant

JAMES WHITE

Assistant to Chairman

HON. CLIFFORD SIFTON
Chairman
Commission of Conservation

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PART I

Development

I

INTRODUCTION

Problems to be Solved.—A knowledge of the normal development of a young oyster from the egg is of fundamental importance in formulating any rational scheme of artificial oyster propagation, as well as in framing suitable laws for the protection and encouragement of the oyster industry as a source of wealth to the country. This, the economic aspect of the subject, is a sufficient excuse for the devotion of time, labour and expense in the acquisition of useful information.

Another aspect, that from the standpoint of pure or theoretical zoology, views each newly acquired fact as a contribution to the total aggregate of human knowledge, taking part in the proof or disproof of some theory, and, in a measure, correcting our conception of a comprehensive philosophy of nature.

Oysters have been known and used as food from the periods of the empires of Greece and Rome; in many countries methods of culture have been employed; they have been studied by some of the greatest naturalists; there is an extensive literature relating to them. Notwithstanding all this, our ignorance of the oyster is astonishing. We have not a single concise, direct, intelligible, true and satisfying account of *where*, *when* and *how* an egg becomes an oyster. To say that oyster eggs, spawned into the sea in summer, grow into new oysters, is not satisfying. We want to know what parts of the sea, what depth of water, how near shore, whether on the surface or on the bottom; if free in the water or hidden under rocks, plants or other objects; whether in stagnant or running water; the temperature, salinity and purity of the water; the character of the bottom; the plants and animals of the region; and, it may be, a hundred other things about the *place* where oysters abound. We would like to know the month, week, perhaps day, when oysters emit their eggs; whether there is a uniformity of action in this among oysters of the same place, or of different places or different years; whether they

are compelled by internal or external forces to spawn at a definite time, irrespective of cold or warm seasons or stormy or calm seas, or if they have the power to await a favourable time, or even to refuse to spawn; whether a noise, tremor, odour or touch from one spawning oyster communicates an uncontrollable impulse to others; and scores of such questions about the *time* when oysters discharge their eggs. We desire to know the size, shape, colour, structure and activities of the egg, and of every succeeding stage in development until the new individual grown up from the egg is as complete as the mother individual that produced it; to know how long it takes for the growing organism to reach each clearly marked change of structure or of habit; to be able to distinguish it at every step from the young of other species; to understand the physical and biological conditions surrounding, influencing or occasioning its existence as egg, embryo, larva, spat, or adult; and a thousand related circumstances connected with the *manner* in which the egg becomes an oyster.

Difficulties of Research.—To many of such questions answers have been given that are fairly correct or are reasonable guesses, partly wrong or absolutely false; to some no answers have been offered, while in the case of others the questions themselves have never been propounded. It has not unfrequently happened that opinions current in less critical ages have been allowed to pass unchallenged into modern literature, and sometimes men have been more intent in recording themselves among the authors on the subject than in gaining a practical acquaintance with the subject itself. This renders the literature cumbersome, and compels future investigators to waste much time in rummaging through worthless publications, for the sincere student desires to know, and to give credit for, what has already been done, as well as to make use of it in planning his own researches. He is compelled to estimate the value of each article in the light of his own experience, and, by comparison with the most reasonable statements of previously published records, to judge by internal evidence of the opportunities and qualifications of its author.

To reach this ideal requires years of faithful work, and no man can understand so well his own limitations, or the difficulties that arise, as the one who earnestly tries to advance our knowledge on any problem that has engaged the attention of hundreds before him. Time after time questions arise and assume such importance as to appear to be the key to the whole subject, but, when answered, sink in significance relative to others that are suggested; the investigator changes the direction of his research, adjusts his methods, and awaits results pointing towards his next move. Each change of plan may call for new apparatus, a different field of experiment, and considerable time to give a fair trial. The bringing together of men of sound training and suitable experience, of literary records of what has already been accomplished, of necessary apparatus

and assistance, upon a well selected spot, at a properly judged time, duly authorized and financed, is a stroke of fortune which falls to the lot of few investigators. Add to this all the dangers, risks, accidents, delays, losses, or other unfavourable circumstances occasioned by adverse external physical conditions, storms, irregular seasons, boats, engines, apparatus, and the like, together with the intrinsic difficulties of the problems themselves, and some conception of the reason why we know so little may be grasped by the layman, indeed he may feel a degree of satisfaction that we have been able to learn so much.

Literature—"A Bibliography of Publications in the English Language Relative to Oysters and the Oyster Industries" (See Bibliography, 1894), gives the titles of 546 separate publications between the years 1665 and 1894, only 28 of which antedate the year 1850. Eliminating those devoted to anatomy, distribution, culture, gastronomics, greenness, resting position, the happiness or the morals of the oyster, odes to an oyster, popular natural history society and magazine articles that do not represent original research, extracts, synopses, reprints that repeat but do not add information, and other rather unimportant or irrelative types of literature, we find that the effective contributions are wonderfully reduced in numbers, although it may be as Horst has stated (1884) that "more has been written on the history of the development of the oyster than on that of any other invertebrate."

Broadly speaking, we may state that our knowledge of the development of the oyster began to be acquired in Europe by at first somewhat vague, disconnected, and scrappy observations on the European species (*Ostrea edulis* L.), in some of the most progressive countries bordering on those parts of the Mediterranean sea, the Atlantic ocean and the North sea, where this oyster abounds. Italy, England, Holland, Denmark, France, Germany, and some other countries made irregular, occasional contributions until, at a later time, corresponding with a greater degree of national peace, leisure, desire for knowledge, need to make use of natural products, improvement of instruments, and design in methods, such isolated, superficial, quaint observations as those of Sprat (1669) gave way through Brach (1690), who first used the microscope to observe the eggs and larvæ of the oyster, Leeuwenhoek (1695), who discovered the spermatozoa and the velum, Baster (1759), Home (1826), to Davaine (1852), who was the first to offer a detailed account and observed the nucleus, blastomeres, shell, liver, intestine, branchiae and heart, and to Lacaze-Duthiers (1854), who in some respects supplemented the preceding, found the mouth and anus, lower lip and otoliths. Then followed Coste (1861), De la Blanchère (1866), Gwyn-Jeffreys (1869), Saunders (1873), Salensky (1874), Möbius (1877), Bouchon-Brandeley (1882), Horst (1882, 1884), Hubrecht (1883), Huxley (1883), and Hoek (1884), of which the papers by Horst and by Huxley mark a distinct progress for completeness and accuracy.

Already the scene of greatest activity had changed to America, where Brooks (1879), Ryder (1881), Rice (1883), Winslow (1884), Jackson (1888), Nelson (1888), and others, accessible to the greatest natural oyster-producing waters of the world, enthusiastically entered into the details of development, artificial fertilization and culture of the American oyster (*Ostrea virginica* Gmelin).

Sexes Distinct in American Oyster.—Unlike the hermaphrodite European oyster, in which the eggs and early stages of development are retained within the mantle cavity of the parent until they reach a size of 0.15 to 0.18 mm. and have a shell, the unisexual male and female American oysters expel their spermatozoa and ova into the sea water, where fertilization and all stages of development take place.

This discovery, due to Brooks, together with his sound scientific methods, set a new standard for research, added immensely to our comprehension of the earlier stages of development, opened a way to progress in artificial culture, and communicated an enthusiasm to co-

workers at home and contemporaries abroad. His works have ever since been regarded as standard on those parts of the subject dealt with, and have been extensively copied, with little inclination to either verify or extend them.

Occasion of the Present Work.—In Canada, the study of the Atlantic oyster began when our movable Biological Station, in the fifth year of its existence (1903), became located at Malpeque, P.E.I., the most important centre of our oyster fisheries. There was assembled the largest staff of investigators ever present at one time at the station, and to each was apportioned his part in the schedule of research. My own part seemed to promise little and had to do with the more mechanical work of boating, collecting, experimenting, and, incidentally, of continuing the study of faunas previously carried on at St. Andrews, N.B., and Canso, N.S. During the first summer a good deal was learned about the local physical environment, form-variations, habits, food, bacteria, associates, and such like things connected with the life of adult oysters; but nothing of importance was accomplished in connection with the embryology. Some attempt was made with a view to determine the period of ripening of the eggs, and to artificially fertilize them, as well as to procure young spat, but these attempts did not furnish even a local orientation with regard to the problems of development.

My own connection with these problems began with the succeeding summer (1904), when I was requested to do what I could in the remaining short season of our stay at Malpeque, for it was understood that the station would be removed beyond oyster areas for the following year's work. Not to have had active experience during the preceding summer, nor to have read the special literature relative to these problems, was a disadvantage which for a time kept me very much in the dark. Naturally I began by applying my knowledge of faunas—macroscopic adult animals, and microscopic adults and young, and the various methods of procuring them. I already knew almost every species of bivalve that could be obtained between tide-marks, or brought up by a naturalist's dredge between low-water mark and fifty fathoms depth, and I had collected myriads of bivalve larvæ in plankton nets. Besides, I had learned to recognize the oldest stages of the free-swimming larva of the mussel (*Mytilus edulis* L.), by comparing the bivalve larvæ of plankton collections with minute mussels found attached to rockweed (Fucus) at St. Andrews, and I thought a similar method might be turned to account in determining other larvæ, perhaps that of the oyster. Accordingly I turned all my energy for a time towards the collecting and scrutinizing of bivalve larvæ in the plankton. At first they all looked pretty much alike, excepting that some were comparatively large and others small; but, after a diligent study of collections from various parts of Richmond bay, it appeared that some were brownish or yellowish, while others were gray, pale and transparent,

and also that some were more pointed at one end than others, or were shorter and deeper. Here then, were differences of size, colour and shape, but I did not know whether they meant numerous different species or different ages of the same or a few species. I then started with one of the largest and commonest, and tried to search out a series descending in size but retaining the same shape, and I found that the smaller (i.e. the younger) were paler and more transparent than the larger (or older) of the same series, but that there were large ones of a different shape that were paler than small ones of this series. A second series was begun for them, and so on, until I had in mind notions of several different species without knowing what species. I reasoned that the mussel (Mytilus), the clam (Mya), the quahaug (Venus), and the oyster (Ostrea) furnished the commonest shells collected, and consequently they were likely to supply the commonest larvæ also. Of these I knew the largest larva of the mussel—of that there was no doubt whatever, for the smallest mussels attached by their byssus to sea-weeds, rocks, weirs, wharves, and such objects, showed narrow, concentric blue rims round a somewhat horn-coloured umbonal area of the same size and shape as the shell of the largest free-swimming larva of the plankton, and by extending one of my series upwards until it connected with this and downwards as far as it could be traced, I not only learned to recognize the mussel at every size intervening between these limits, but removed all these stages of this most abundant larva from the field of question, thus narrowing the problem closer around the oyster. I tried in the same way to eliminate other species, but for them the stages immediately following the free-swimming larvæ are not so easily found as in the mussel. All the while I was extending my series and forming theories, which were little better than guesses, as to what they were and which was the oyster.

A peculiar, opaque, reddish-brown coloured larva, that did not always look the same in shape, sometimes appearing so aberrant as to resemble certain broad-mouthed, low-conical, univalve shells, had been singled out as worthy of special attention. But to prove whether this was the larva of the oyster or not I must obtain the youngest fixed stages (spat) following the largest free-swimming plankton stages. I judged that such stages for the oyster would probably be attached to rocks or shells, whereas the corresponding stages for the clam and quahaug would be free-creeping and burrowing, like their parents.

I examined the surfaces of shells, stones, rocks, stakes, wharves, the superficial ooze, mud, sand, gravel, rock-weed, eel-grass, and everything in fact I could think of in various parts of the bay. But what small bivalves I could find were not small enough for the purpose, because, as a shell grows bigger, the larval shell retained in the region of its umbo becomes weathered, corroded, overgrown, thickened or warped, its valves pressed open, rent apart or otherwise so far distorted in appearance and

position that it becomes difficult and unsatisfactory to make a comparison with the shell of the free-swimming larva. The very youngest spats, that have only a narrow rim of new shell (dissoconch) added to that of the larva (prodissoconch), are likely to be free from any such modification, but I could not find any young enough. The smallest oyster shells I could find at the time were about the size of a man's thumb-nail, which was far too large.

Being blocked in this direction, I next resorted to experiment by putting out bundles of brush tied down or weighted down with stones at likely places for the capture of oyster-spat, and I also recalled the method of putting out glass I had read about while studying the clam at St. Andrews three or four years before. Strips of window-panes were stood in crocks, in favourable places under the water, and looked at every day, each speck that remained after rinsing the glass in sea-water being examined with a lens and, if need be, with a microscope.

In this manner, in due time, I caught a young spat, so close after its fixation that there was little change in appearance—its identity with one of my series of free-swimming larvæ being unmistakable. This was the supreme moment that knit all isolated observations into one fabric and turned guesses into facts. The peculiar larva already mentioned was an oyster larva, and this was an oyster spat, and, moreover, the present was the period when the developing oyster changes both its habits and its structure. Plankton had been collected since the first week in July; the oyster larva had been under suspicion since the 25th of July; and now the first oyster spat was captured on the 16th of August.

There remained but to verify and fill in details. Spat increased in numbers and size and were soon to be found on shells and stones, while on the contrary the larvæ became less plentiful and dwindled out early in September.

In 1905 I had the opportunity of studying plankton at Malpeque between the 7th and the 26th of June, and was unable to find any oyster larvæ, so that, putting this along with my previous observations, I felt justified in concluding that July was the month for larvæ and August the month for spat. This and the following summer were spent in Gaspe, Que., the next at Seven Islands, Que., and another back at St. Andrews, N.B., so that I had no further opportunity to verify or extend my observations on the oyster until the summer of 1909, which was devoted to the oyster and quahaug areas of eastern New Brunswick and Prince Edward Island.

In the meantime I had learned to recognize the larvæ of the silver-shell (Anomia), the scallop (Pecten), and the clam (Mya), and had developed accurate methods of measurement and comparison. It being unsafe to rely on sight and memory, I kept records of outlines of larvæ made with a drawing apparatus attached to my microscope, and of measure-

ments of length and depth made by a micrometer. During the last mentioned summer (1909), I added the quahaug (Venus) to the list of known larvæ, reviewed the whole field of oyster development from the egg to the adult, dwelling particularly on the time of ripening of the eggs and spawning, the first occurrence of larvæ in the water, and the first appearance of spat, as well as performing successful fertilization and culture experiments.

During the summer of 1910 I was again stationed at St. Andrews N.B., where I could do nothing more on the oyster; but the greater part of the summer of 1911 was spent at Nanaimo, B.C., where I succeeded in proving that the Atlantic oyster can be successfully cultivated in Pacific waters, and made out the mode of breeding of the little British Columbian oyster (*Ostrea lurida,* Carp.).

II

THE OYSTER AND ITS MODE OF LIFE

Species.—The oyster is classified under the sub-kingdom or phylum of animals called Mollusca—one of about ten such great subdivisions of the Animal Kingdom. Of the four or five classes of mollusks, the one to which the oyster belongs has often been called Bivalvia or Lamellibranchia. In this there are over twenty families, the Ostreidæ being one. Its most typical genus, Ostrea, has been said to contain some seventy living and two hundred fossil species.

Lamarck, in his day, gave brief descriptions of fifty-three living and eighty-two fossil species. He referred eleven living species to America, of which, three are of interest here as occurring on the Atlantic coast of Canada and the United States, namely:

Ostrea virginica, Gmelin, on the coast of Virginia;

Ostrea borealis, Lamarck, near New York;

Ostrea canadensis, Lamarck, at the entrance of the river St. Lawrence and near New York.

The differences are in the size, shape, and surface of the shell, e.g., whether elongate or oblong-ovate, straight or curved, thick or thin, and in the upper valve being flat or convex, etc.

Two papers by White and Heilprin enumerate more than one hundred species of fossil Ostreas for this continent alone.

Those zoologists who have had the advantage of studying living oysters in their natural surroundings and who have extensively collected by hand, by tongs or rakes, and by dredges, on different grounds and from various depths, can easily understand how museum specimens and fossils, dissociated from their companions, may be assorted into many apparently different species. On almost any oyster area it is possible to pick out specimens corresponding to Lamarck's three living species before mentioned and to fill in transitional forms. Most of the oysters at Ram Island point, Malpeque, would be classed as *O. borealis;* many on the Curtain Island beds would be called *O. canadensis*; while numbers of what are locally spoken of as cove-oysters would fall in the type genus *O. virginica.* The small Caraquet oyster is perhaps the most constantly divergent variety on our coast, and, as will be shown later, cross-fertilization between it and the very different large Curtain Island oyster can be effected. It is generally understood now, by those who have given attention to the subject, that there is but one living species (*Ostrea virginica,* Gmelin = *O. virginiana*

Lister) on the Atlantic coast of Canada and the United States. A small distinct species (*O. lurida*, Carpenter) occurs on the Pacific coast of Canada, extending southwards to California.

Distribution.—In geological distribution the genus Ostrea dates from the Carboniferous era, and reached its culmination in the Cretaceous, when two other genera (Exogyra and Gryphæa) became extinct. Geographically, it is to be found in waters adjacent to every continent, but especially to the south and west of Europe, on both sides of America, the east and south of Asia, and south of Australia. The North Atlantic with its extensions into America (gulf of St. Lawrence and gulf of Mexico) and into Europe (Mediterranean, Adriatic and Black seas, bay of Biscay, English channel and North sea) is the great oyster-producing ocean of the world. Japan, China, India, Java, Australia, Tasmania, New Zealand, Brazil, California, British Columbia, and some other countries not within its bounds, have a relatively small production. Nowhere do oysters occupy such extensive, continuous areas as on the eastern coast of the United States, the greatest oyster-producing as well as the most lavish oyster-consuming country in the world. From cape Cod to the gulf of Mexico is one vast, almost uninterrupted area, with Chesapeake and Delaware bays as the centre of most profuse production, and Baltimore as the greatest oyster market in the world.

On the Atlantic coast of Canada oysters occur at many places, from Chaleur bay along the coast of New Brunswick and of Nova Scotia to near the strait of Canso, on both sides of Prince Edward Island, in the Bras d'Or lakes of Cape Breton, and very sparingly at a few places on the south shore of Nova Scotia to the east of Halifax. The centres of greatest production are Miramichi bay, N.B., and Richmond bay, P.E.I.

Habitat.—Oysters occur in shallow bays and estuaries of rivers, where the water is warmer and less saline than that of the sea, and where there is also a greater abundance of suitable food. Adult oysters cannot swim, creep or burrow, but are normally fastened upon the left side to a rock, shell, or other submerged object. As the older oysters die off young ones build upon their shells, until the mass broadens and thickens into a more or less extensive bed. Small, isolated clumps of oysters also occur, and many individuals become broken loose and rolled about by disturbances in the water.

Food.—As the oyster cannot go in search of food, it has to depend upon that which is produced by the water of its immediate vicinity, or brought to it by currents. As it has neither jaws nor teeth, it cannot make use of anything except the smallest particles of food-material. Both of these conditions are met by the vast numbers of minute plants and animals, —particularly the group of the former called diatoms—that swarm in the water and constitute a great part of what is known as "plankton". These

are drawn in with the respiratory current, and swept towards the mouth by cilia on the surface of the gills and palps.

Breeding.—Of our Atlantic oysters, males and females occur in approximately equal numbers. Each individual, when sexually mature, has an enlarged reproductive organ, situated inside the body and surrounding the stomach, liver and intestine. This organ has two outlets, one on each side, near the posterior end of that part of the abdomen which projects backwards, below the great adductor muscle. Each outlet is the open end of a duct, which runs forward and divides into branches that spread, tree-like, over the side of the body, on their way to the various lobes of the reproductive organ.

In the female this organ is the ovary, and its duty is the preparation of specialized cells, the ova or eggs, which, as they ripen, are pressed outwards through the already mentioned duct—the oviduct. Ova are generally extruded in large numbers at a time, constituting the spawn or roe, while the process of extrusion is known as spawning.

In the male the reproductive organ is the testis or spermary, its duct is the sperm-duct, the specialized cells are sperms or spermatozoa, being also called milt.

Eggs are spherical, oval or pear-shaped cells of about 1/500 of an inch in diameter, and are barely visible as separate particles to the unaided eye.

Sperms are extremely small—it would take several thousand to make up the mass of an egg—and somewhat resemble minute pollywogs, in that each has a body and a tail and is capable of independent swimming movements.

When eggs and sperms are spawned into the water on an oyster-bed, many of the eggs are soon met by sperms, one of which may succeed in penetrating into each egg. This is, in brief, what is usually called fertilization.

The fertilized egg undergoes rapid internal changes, which soon result in its division into two cells instead of one, but remaining in contact and forming one object. Further divisions speedily follow, until the cells become so numerous, their structure so varied and specialized, and their arrangement so orderly that an organized living animal and eventually an oyster is the result.

The setting apart from the bodies of a pair of adults (male and female) of a pair of special cells (ovum and sperm) which unite (fertilization), the product ultimately becomes a new individual, is sexual reproduction—the only method of breeding and increasing the number of individuals of oysters.

III

REPRODUCTIVE CELLS

Embryology.—The study of the manner in which reproductive cells, through multiplication, specialization and organization, incorporate new matter and energy and grow into new individuals similar to their parents is embryology, ontogeny or developmental history. This is the main subject of Part I of the present work.

As a brief forecast of the process of individual development it may be stated that it begins with the fertilized *egg* or *oösperm* (ova-sperm, Plate I, fig. 1) as the simplest form in gross structure assumed by the individual at any period in the whole cycle of its life-history. The oösperm by successive divisions soon gives rise to a simply constituted cellular organism, the *embryo* (figs. 2–8), and shortly afterwards to a more highly organized, swimming and creeping, feeding and growing, young animal, the *larva*, (figs. 9–21). At the end of a period of free life the larva settles on to some solid object, such as a rock or shell, fastens its own minute shell thereto, and becomes a *spat* (fig. 22), which has but to grow (Plates II and III) and complete its organs to become an *oyster*. When it reaches a size of about one inch in length (Plate III, 4th line and 1st fig.) the young oyster begins to produce sperms or eggs (Plate VII, fig. 20) of a new generation. Egg, oösperm, embryo, larva, spat, oyster, and again the egg, are the chief stages in the cycle of development.

Any account of the development of the oyster always remains to some extent imperfect. What is regarded as complete for the time is obtained by fitting each newly acquired fact into its proper place among those already known, in such a way that the whole makes a continuous and reasonable story. The progress towards completeness in the narrative is as much a development as are the events described.

The older naturalists, zoologists, or embryologists had to content themselves with few facts and employed but few descriptive terms. The meaning of the word "egg" was often extended to include embryonic and even larval stages; the word "embryo" comprehended larva and even spat; "spat" was applied to swimming as well as fixed stages. This indefinite mode of description corresponded with the knowledge of the time. When we consider the inexperience, disadvantages, want of appliances and lack of methods, we can freely forgive their errors and feel grateful for the information and theories they passed on as a guide and incentive to further research.

But when we turn to works of the present day we look at least for sufficient research to distinguish facts from fancies, as well as for a plain, direct and unambiguous statement of observations and their apparent bearings—in short, for a scientific method. Some of the hastiness of observation and conclusion, as well as looseness in the application of terms, in America, comes from a too confident expectation of the same conditions and phenomena as have been observed in Europe and the application of terms already in use in European literature.

Our oyster is of a different species from the European oyster and there are some remarkable differences in the development. The most important of these is that in our oyster the ripened eggs are discharged at once into the sea, outside of the mother oyster, where fertilization and all stages of development take place. In the common

European oyster, on the contrary, the eggs, after passing from the ovary, and oviduct, are retained for some days in the mantle cavity of the mother, where development progresses through the oösperm, embryo, and young shell-bearing stages that are also capable of locomotion, the latter being finally passed out into the sea as actively swimming larvæ, protecting themselves and finding their own food. These, while retained within the mother, may be excusably called embryos, but not larvæ; after they take to an independent life they are larvæ, not embryos. The term 'spat" appropriately applies to the succeeding fixed condition as resembling spit (i.e. spittle).

In accordance with the preceding, it may be pointed out that the word "embryology" is itself less suitable as a title for the present paper than the much broader term "ontogeny" which, because of its unfamiliarity, is often supplanted by the expression "developmental history," or simply "development."

It is impracticable to procure eggs, oösperms, or embryos as they occur in the natural course of development in the sea; to obtain them in numbers and with facility it is necessary to turn to artificial means, beginning with sexually ripe male and female oysters.

The Sexes.—The oysters of eastern Canada are diœcious or unisexual, i.e., there are two sexes, every individual being either male or female. Males and females cannot be distinguished externally. To determine the sex it is necessary to sacrifice the life of the individual by breaking apart the two valves of the shell. After some experience it becomes possible in most cases to recognize the sex by observing the surface of the abdomen, provided always that the individual is sexually mature and its reproductive elements are approaching ripeness. At such a time the abdomen presents a plump and milky appearance, whereas in immature specimens and those that have already spawned, it is either shrunk, flabby and opaque, or else it is distended, watery and semi-transparent. Coarseness of the ramification of ducts on its surface, as well as a creamy colour and distinct granulation, are indicative of femininity. By stroking the abdomen backwards it is often possible to squeeze spawn or milt out of the opening of the oviduct or sperm-duct, in much the same way as fishes may be "stripped." In case the specimen is not quite ripe it is necessary to puncture the abdomen or one of the larger ducts and extract a little of its contents. In viewing this again it is generally possible to decide with the unaided eye, for eggs in mass are yellower in colour and coarser in granulation, while spermatozoa are whiter, with a very fine or more homogeneous appearance. But the surest way, as well as the most expeditious, is to transport on the point of a scalpel a small portion of the spawn or milt to a drop of water on a slide and observe it under a microscope. Ripe eggs or sperms readily separate and float out into the water, facilitating a clear view of their size, shape, structure and activities. From their characters the sex is determined.

Eggs and Sperms.—Under a low power of the microscope, *eggs* (Plate V, fig. 1) appear to be somewhat large objects, of a spherical, oval, pear-shaped or even more irregular form. The more spherical ones (fig. 3)) measure about .05 millimetres (= 1/500 inch) in diameter, each limited by a membrane (vitelline membrane, cell-wall,

shell) with an underlying, thin, transparent layer of homogeneous protoplasm (ectoplasm), inside of which is a more opaque, granular mass (endoplasm), containing a central globular vesicle (nucleus) with a distinct spot (nucleolus). The granules of the endoplasm are mostly of the nature of yolk (deutoplasm), a sort of concentrated food-matter and store of energy to be drawn on during the earlier stages of development, before the organism possesses a mouth or is capable of taking up the ordinary food of the oyster. Between the granules and around the nucleus is clear, active cytoplasm, similar to the ectoplasm. The nucleus is bounded by a membrane and contains transparent nucleoplasm, in which are embedded the globular nucleolus, together with other smaller bodies called chromosomes, the latter believed to be the bearers of hereditary characters from parent to offspring. There are still other structures in the egg, some of which are constant and some that appear only at intervals, for the living egg is an active, changing organism, although it does not make this evident by locomotory movements. Most of these structures are first clearly exhibited after treatment with some chemical reagent or staining fluid, which of course interferes with or entirely arrests the natural activities of the egg. The protoplasm has a supporting network of extremely fine fibres; there is a sort of cell-sap in which yolk granules may become dissolved and diffused when required to any part of the egg; there are chromatin granules, centrosomes, and other particles.

Sperms (spermatozoa), when viewed under ordinary low powers of the microscope (Plate V, fig. 2), such as are sufficient for the distinct recognition of eggs, appear as mere specks or at most as minute, bright globules, with a quivering movement, due to the rapid vibration of their tails, which may not at first be visible. To study their size, shape, and structure requires the highest powers and best devices of the microscope.

The work contained herein was done with a Leitz Ia microscope, Abbé condenser, iris diaphragm, triple nose-piece, oculars I, III, IV, V, objectives 2, 4, 7, $\frac{1}{12}$, oil immersion (greatest magnification 1250 diameters). Measurements by an ocular micrometer (5 mm. = 100 parts), valued by a stage micrometer (1 mm = 100 parts).

To make the measurements more intelligible the following table is inserted showing the actual values in micra of one of the smallest divisions of the ocular micrometer (in ocular V) with each of the objectives:—

Oc. V, Obj. 2—65 oc. mic. = 100	stage mic. = 1 mm.	= 1000 μ *
1		15·38 μ
4–100	69	$\frac{1000}{100} \times \frac{69}{1}$
1		6·9 μ
7–100	14.5	$\frac{1000}{100} \times \frac{14\cdot5}{1}$
1		1.45 μ
1/12 – 80	7	$\frac{1000}{100} \times \frac{7}{1}$
1		.875 μ

*The Greek letter μ is used to denote the one millionth part of a metre, known as a 'micron' (plural 'micra').

In measuring with such small units the larger the measurement the more correct it is, for the difficulty of reading one or two units where even the thickness of the micrometer lines has to be considered, is liable to cause as great an error for one or two units as in other cases would be spread over a great many. Spherical eggs measured with Oc. V, obj. 4, give nearly $7\frac{1}{2}$ ($7\frac{1}{2} \times 6{\cdot}9 = 51{\cdot}75\ \mu$); with Oc. V, obj. 7, they vary about 35 ($35 \times 1{\cdot}45 = 50{\cdot}75\ \mu$), while the head of a sperm-cell with Oc. V, obj. $\frac{1}{12}$ is approximately 2 ($2 \times {\cdot}875 = 1{\cdot}75\ \mu$).

Each spermatozoön (Plate V, fig. 4) possesses two distinct parts, a head and a tail. The head is almost oval in form, somewhat pointed anteriorly, but inclined to be squarish posteriorly, where there are four minute spherules, between which is inserted the tail. The head measures approximately .00175 mm. in breadth, while the tail is fully twenty times this length, becoming so fine towards the end as to be hardly perceptible. A sperm-cell is much more highly specialized than an egg-cell, i.e., it differs more markedly from a typical young, living cell of the body, and this is in adaptation to the special work it has to perform. It resembles in shape and behaviour many fully organized, active animals. Its ability to swim by violent flapping of its tail, its small size, and the vast numbers produced, increase the chances of its coming in contact with and penetrating into an egg. Most of the head consists of nucleus, about which the protoplasm is reduced to a minimum, and its brief life as an independent organism does away with the necessity of its being encumbered with food granules. Notwithstanding the fact that we are accustomed to think of the egg only as passing by development into the larva, yet it would seem that the sperm is just as important, and it is due to its relative inconspicuousness and early disappearance that we forget it. Unfertilized eggs soon die and disintegrate; it is only healthy eggs, normally fertilized, that develop. The sperm infuses new life and vigour, and, besides, it is the only means of carrying over hereditary characters of the male parent to the offspring.

Fertilization (Fecundation).—The male reproductive organ (testis) occupies a like space in the body of the male oyster as does the female reproductive organ (ovary) in the body of the female, and we would judge that the male discharges an equal mass of reproductive matter. Examination of large numbers of full-grown oysters shows that the sexes are approximately equal in numbers; as a consequence there would be several thousand sperms for each egg spawned. This difference is further increased by the circumstance that males become sexually efficient at an earlier age than females. In the water about every oyster bed, in the breeding season, the number of spermatozoa must be inconceivably great—doubtless a provision of nature to insure that each egg shall have a fair chance of becoming fertilized. It would look at first sight as if there were little risk in this respect. But we must stop to consider that many males may expel their spermatozoa when and where there are no eggs to be fertilized, that the active life of a spermatozoön is limited to a brief period,

that millions of them must go astray in the mud, stick fast to objects, be swallowed by oysters themselves as well as by other animals, or become drifted away by the ebb and flow of the tide.

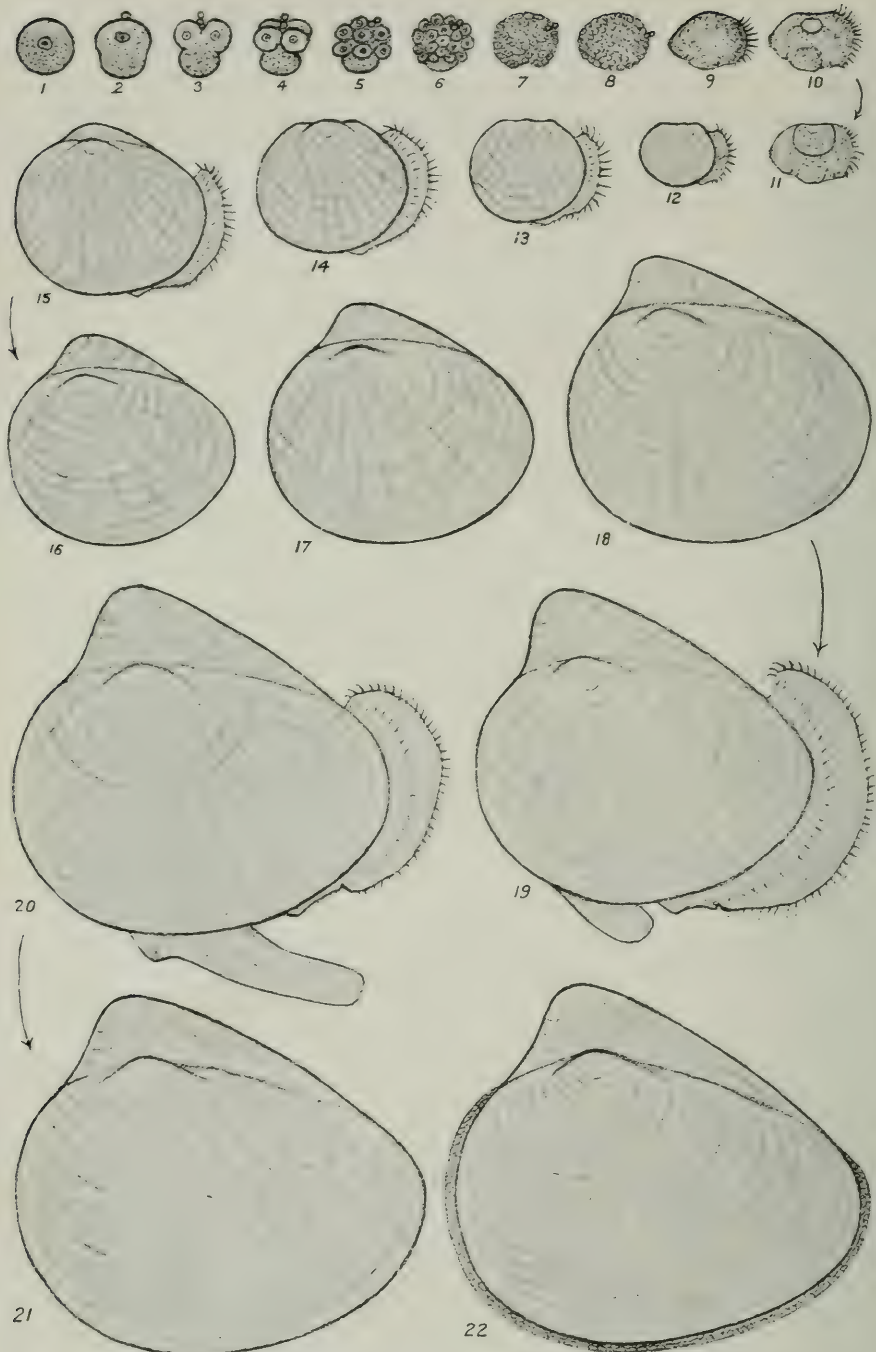
Eggs are subject, in a less degree, to similar adversities. They have no power of locomotion, and while they may be swept about and kept in suspension for a time, yet, as can be seen by mixing a quantity in a tumbler of sea-water and letting it stand, most of them must sink to the bottom, where many, in the natural course of events, become smothered in moving sediment, crushed, eaten, or otherwise destroyed. To those that remain suspended for some time there are the chances of being carried out to sea on the one side or of being thrown up on the beach on the other. These are types of the first accidents in a long series, that menace the existence of the progeny at every step from the time of liberation from the parent to the time when the more fortunate are themselves occupying the position of parents.

The study of fertilization may be advantageously begun by selecting ripe male and female oysters, and, by a process of stripping into tumblers of sea-water, securing first a stock of normal, healthy, unadulterated eggs and sperms. Rougher methods, such as the extraction of the reproductive, organs, or the chopping up of the bodies of the oysters, carry over a mass of undesirable, injured tissues, which interferes by smothering or decay and is difficult to get rid of. Eggs and sperms may be mixed in any proportion on a slide, in a watch-glass or in a tumbler, transfer being effected by a medicine-dropper, a glass tube, or, when in large quantities, by pouring. The chief care required is in the temperature, for small, isolated portions of water are liable to become quickly warmed above that of the sea. When large quantities of eggs are used and required to be kept for developing stages, the mass of eggs and sperms should be gently stirred for a few minutes, to allow free access of the sperms to the eggs. Then by repeated settling of the eggs, pouring off of impure water and addition of fresh sea-water, the fertilized eggs and segmenting stages may be kept in healthy condition.

Within about ten minutes after the addition of sperms to a quantity of eggs almost every egg will be found to be dotted with sperms, that are either helplessly clinging to its surface or are energetically attempting to bore their way into it. This they are unable to do, with the exception of the one perhaps, which is fortunate enough to strike the receptive spot (Plate V, fig. 5) or point where the egg membrane is so thin as to permit easy ingress to the protoplasm. The receptive spot in this case is equivalent to the micropyle in many thick-walled eggs of other animals, and is situated, in pear-shaped eggs, at the point. Fertilization is not completed with this impregnation and disappearance of the sperm into the egg. The protoplasm of the egg furnishes a suitable medium for the carrying out of complex processes that result in the intimate mingling of the chromo-

somes of both egg and sperm nuclei. To follow these processes requires the employment of highly technical methods and turns the attention from the more superficial phenomena of gross structures to a penetration into the more profound constitution and intrinsic activities of living protoplasmic units. An egg-cell contains so many minute parts and undergoes such rapid internal changes that it is impossible to watch all that goes on. The aggregation of yolk-granules in the protoplasm especially obscures the vision and even materially interferes with or modifies the processes themselves. These difficulties are largely overcome by making great numbers of observations on living eggs, some of which are more favourable than others; by preserving eggs with chemical reagents at various stages and then using different agents to stain and to clear until otherwise invisible parts are rendered apparent; by comparison with more transparent eggs of other animals; and by resorting to a method of sectioning of eggs large enough to permit it.

There are in the protoplasm of the egg at this period two bodies of such special activity as to be considered of commanding importance, the original nucleus of the egg and the transported head of the spermatozoön. Each begins separately a series of changes preparatory to their union. Those changes which belong especially to the egg and its nucleus are regarded as a process of maturation. A mass of clear protoplasm about the nucleus separates into two portions (astrospheres) which become star-like and moved to opposite poles of the nucleus (Plate V, fig. 6). At the same time the nuclear membrane and nucleolus disappear, leaving the chromosomes free. Rays of the astrospheres diverge in all directions from two central bodies (centrosomes), some of them extending outwards through the protoplasm to the ectoplasm, others stretching inwards to become attached to chromosomes. Contraction waves pass over the surface; the egg-membrane becomes wrinkled as if the ectoplasm were being pulled away from it; a quivering motion of the protoplasm is observable; the astrospheres and chromosomes are carried towards the pole of that hemisphere of the egg which becomes the larger. Those rays which lie along the axis between the two centrosomes form a nuclear spindle, and by contraction the chromosomes are divided into two groups. One of these groups is thrust outwards, carrying with it portions of an astrosphere, protoplasm and egg-membrane, which constricts around and separates the mass as a small globule (first polar globule) on the surface of the relatively large egg (fig. 7). A nuclear spindle is reconstructed within the egg, the chromosomes again divided, and a second polar body soon formed at the base of the first (fig. 8). In the eggs of some animals it has been observed that the chromosomes become split longitudinally into double their number during the formation of the first polar body, and that this polar body divides, each part taking half the chromosomes during the formation of the second polar body. This would seem to show that the



EGG—EMBRYO—LARVA—TO YOUNGEST SPAT
(Enlarged 150 times)

KEY TO PLATE I

All the figures of this plate are drawn as accurately as they admit of, to the same scale of magnification, viz., 150 diameters, so that the relative sizes of different stages may be seen at a glance. They are also oriented in the same position throughout, with the dorsal margin upwards and the anterior end to the observer's right, i.e., they lie on the left side like the attached oyster.

Fig. 1. Oyster's ovum. Oc. 5, obj. $4 = 7 \cdot 5$ of the ocular micrometer scale, of which each unit in terms of the known stage micrometer is $6 \cdot 9\mu$.

$7 \cdot 5 \times 6 \cdot 9 = 51 \cdot 75\mu \cdot = \cdot 05$mm.

$(\cdot 05 \div 25 = \cdot 002$ inch $= 1/500$ inch).

$\cdot 05 \times 150 = 7 \cdot 5$ mm = the size of the figure.

Figs. 2–8. Segmentation and formation of the embryo.

Figs. 9–21. The larva.

Fig. 22. The youngest spat.

Fig. 2. Extrusion of the first polar body and lengthening of the oösperm.

Fig. 3. First (partial) cleavage into two blastomeres (micromeres) above, with the uncleft deutomere below.

Fig. 4. Second cleavage at right angles to the first, giving rise to four micromeres.

Fig. 5. Early stage of the morula.

Fig. 6. Later stage of morula or beginning of the blastula, with the deutomere still observable.

Fig. 7. Early gastrula.

Fig. 8. Later gastrula.

Fig. 9. Trochophore or first stage of the larva, with its swimming organ—the prototroch. The animal now begins to swim, swallow food, and grow.

Fig. 10. Beginning of the shell.

Fig. 11. Growing shell.

Fig. 12. Shell sufficiently large to enclose the body but not the prototroch. Larvæ may be raised to this stage from artificially fertilized eggs. Larvæ of this stage may also be caught by the plankton net in oyster waters early in July. Shell: length 10, depth 8, straight hinge-line 5.

Fig. 13. Shell 15 x 14: 7. The prototroch is now a retractile velum.

Fig. 14. Shell 20 x 18. Beginning of the umbos.

Fig. 15. Shell 25 x 23.

Fig. 16. Shell 30 x 28. Velum retracted within the shell.

Fig. 17. Shell 35 x 32.

Fig. 18. Shell 40 x 38.

Fig. 19. Shell 45 x 42. Velum and tip of foot protruded.

Fig. 20. Shell 50 x 46. Foot protruded.

Fig. 21. Shell 55 x 48. Full size of the larva. Sizes larger than this are seldom taken in the plankton net, showing that at this stage most larvæ either become attached or are destroyed.

$55 \times 6 \cdot 9 = 379 \cdot 5\mu = \cdot 3795$ mm. $= 1/66$ inch.

Fig. 22. Spat of a few hours' fixation, with a narrow rim of spat shell (dissoconch) built on to the lower border of the larval shell (prodissoconch). This stage is difficult to find on natural objects (stones, shells, etc.), but may best be obtained on clean surfaces such as glass intentionally put out to capture them about the middle of August and later.

whole process represents a twice-repeated cell-division, resulting in one large cell (the matured ovum) and three small polar cells (not often completely divided), that, on account of their small size, appear to arise by a process of budding from the egg; also that each of the four cells contains only half the normal number of chromosomes for somatic cells of the same animal, and, since the polar cells take no further part in development, the matured egg has come into possession of a greater amount of protoplasm, with its store of yolk, but only half the number of chromosomes, which form into a new nucleus of smaller size—the female pronucleus (fig. 9).

Coincidentally with these events, belonging properly to the egg, there are also processes, partly parallel with them, taking place in the transported head of the sperm-cell. In spermogenesis, as well as in oögenesis, there are three periods, proliferation, growth, and maturation. The first two in the case of the egg, but all three in the case of the sperm, take place in the reproductive organ of the parent, so that maturation divisions in the latter case only contribute to increasing the number of spermatozoa, since there are no sterile, degenerate polar bodies among them, those cells corresponding to polar bodies maturing into sperms and quadrupling the number of the latter. The tail of the impregnating sperm either drops off at the surface of the egg or becomes absorbed into the egg-protoplasm. The head becomes changed into a nucleus—the male pronucleus (fig. 9)—and it is believed the neck or point of insertion of the tail carries over a centrosome, which becomes active in the formation of an astrosphere. Male and female pronuclei become attracted to one another along a new spindle, meet and fuse about the middle of the egg, and out of them a new nucleus is constructed—the segmentation-nucleus (fig. 10)—of normal size and number of chromosomes, of which half are descended from the ovarian ovum and half contributed by the sperm. The process of fertilization is now complete, the product being a fertilized egg (oösperm, oösphere), which, as shown by its subsequent history, is a very different thing from an unfertilized egg, that will not develop.

In contemplating the foregoing process it is impossible to disregard the manner in which all parts of the egg seem to be under control, the mechanical way in which some bodies are moved about, and the physico-chemical methods by which others are dissolved and reappear. Another point of interest is the reduction of egg and sperm chromosomes to half the normal number for the species, thus apparently necessitating the union of elements from two different parents, with all their hereditary potentialities. Some zoölogists may see in this an internal means of bringing about variations among individuals, leaving to natural selection the task of preserving those variations that constitute the best adaptations to external conditions.

IV

DEVELOPMENT PREVIOUS TO THE SWIMMING STAGE

Oösperm and Segmentation Stages.—As soon as fertilization commences the egg takes on a more spherical shape, but the oösperm, one or two hours later, lengthens again in the same direction as is common among fresh unfertilized eggs. Oriented in the position in which the heavier yolk-bearing portion is below and the more protoplasmic portion carrying the polar bodies above (Plate I, fig. 2; Plate V, fig. 10), the oösperm possesses polarity, the lower pole being especially nutritive (vegetative, vitelline), the upper formative (animal, protoplasmic). The more unwieldy yolk has a retarding influence, which finds expression in the very first efforts at segmentation. Instead of there being an equal division into two completely symmetrical hemispheres, the first cleavage affects directly only that portion which belongs to the formative pole (Plate I, fig. 3; Plate V, fig. 11), with the result that two almost equal blastomeres are formed, below which is suspended an undivided mass, containing most of the deutoplasm, adhering rather more closely to the larger blastomere. This mass itself resembles a blastomere and may be conveniently spoken of as the deutomere. The constricting furrow deepens until the figure presents three rounded lobes in one plane and meeting at one point, while the polar globules are retained in the furrow between the two smaller lobes above. After the first energetic efforts at division the furrows relax until the larger of the two blastomeres completely re-unites with the deutomere (Plate V, fig. 12), the whole remaining for a time in a resting condition (resting period). The figure then presents the appearance of a small blastomere (micromere) budded off from a large one (macromere).

The second cleavage likewise affects only the formative pole, dividing the two blastomeres—which re-emerge—through the insertion of the polar bodies, in a direction at right angles to the first cleavage (Plate I, fig. 4; Plate V, fig. 13). One of the halves of the larger blastomere again retains more intimate connection with the deutomere, giving the latter a slightly excentric position. The blastomeres can now no longer be brought into a single plane with the deutomere, but form a horizontal plane of their own, and the only vertical plane that can divide the whole into equal halves falls through the deutomere, the blastomere above it, and the middle one of the other three, most clearly seen in the resting period which follows.

The third cleavage is restricted to a smaller mass than the first and second, and also appears to be subject to a greater variation. It may occur that the two descendants of the smaller of the first two blastomeres divide, or it may be that division is at first confined to only one of these, viz., the middle one of the three most completely detached from the deutomere (Plate V, fig. 14), Irregularity may even begin in the second cleavage, in that the larger of the two original blastomeres does not keep pace with the smaller one. In any case segmentation advances most rapidly among the descendants of the first micromere, followed closely by those detached from the first macromere. The blastomeres can not preserve a horizontal plane, but curve over the deutomere (Plate I, figs. 5, 6), so that it soon becomes impossible to keep track of the planes of cleavage. The polar bodies and the deutomere serve as landmarks for orientation, and it is possible, in a general way, to observe the direction and manner of progress. Although the first cleavage began with an equal division, the result at the end of the succeeding rest was a large macromere and a small micromere resembling a bud. Similarly the second cleavage effected the division of the micromere and the formation of another bud. In this way the deutomere becomes reduced, and the number and extent of the small blastomeres increased until the latter form a cap over and partly surrounding the ever diminishing deutomere, which, after a time, is withdrawn into and almost enclosed by the cap, where it finally divides into two equal cells (Plate V, fig. 19).

Embryonic Stages.—With the series of cell-divisions and the simple arrangement of the blastomeres the resulting structure has come to be a very different object from the solid sphere with which it started. From the time of the first cleavage it is no longer an egg, nor an oösperm; it is in the strict sense an embryo. At first the cells are everywhere close to one another, soon forming the stage corresponding most nearly with what has been called the morula or mulberry mass in many other animals. By mutual pressure each cell tends to keep to the surface, occasioning more or less of a space in the centre of the mass, but never forming a typical blastula (blastosphere). The remnant of the deutoplasm presses into and occupies most of this space, where it divides first into two, but soon into a few cells, that are larger than those on the surface. They arrange themselves into a layer arching inwards with a depression open to the outside on the lower, somewhat flattened surface of the whole structure, which is now a gastrula (Plate I, fig. 7; Plate V, fig. 19, 20). The cap of small cells forming a single layer on the outside constitutes the ectoderm (epiblast); the inwardly arching layer of larger cells is the endoderm (hypoblast); the space between the two layers is the segmentation cavity (cleavage cavity, primary body cavity, von Baer's cavity, blastocœle); while the depression on the under surface is the widely open gastrula mouth (blastopore). With the formation of this double layer of

cells, to some extent resembling two cups set one within the other, but continuous at their rims, the embryo begins to assume a low grade of tissue organization, for the outer layer naturally has to contend with the more physical relations of the external world, while the inner takes up the more chemical work of digestion. A portion of the yolk was distributed to the protoplasm of each cell as it was formed, but the richest supply was divided up among the endoderm cells. Continued cell-division now deepens this endoderm into a primitive gastric cavity (archenteron, cœlenteron, Plate V, fig. 21), as well as extends the ectoderm around to narrow the blastopore. The polar bodies may still remain and serve as a landmark for orientation; but, due to the most rapid division in the region of the smaller of the first pair of blastomeres, the polar bodies have come to be carried in the opposite direction, and the long axis of the embryo begins to change from vertical to transverse. Cilia appear on the ectoderm cells (Plate I, fig. 9; Plate V, fig. 21) and the little organism now undertakes swimming movements characteristic of a post-embryonic period of life, distinguishing it as a larva.

Division of cells must be considered to be always preceded and governed by nuclear division analogous to that referred to in the formation of the polar bodies; in fact the presence of a nucleus is the surest proof of cellular structure. The nuclear spindle is formed in the direction of the longest axis of the protoplasmic mass and the plane of cleavage of the protoplasm is transverse, through the centre of the nuclear spindle. Judged by this test it would seem uncertain whether the body originating in the first cleavage and hitherto spoken of as the deutomere is a true blastomere. Brooks, whose description of the external features of segmentation seems to be most complete, was unable to follow the phenomena of nuclear division. In his work of 1880 he speaks of this mass as a macromere in contradistinction to the two small cells (micromeres). Nelson (1901), who devoted much time to nuclear structures, speaks of the same mass as a yolk-sphere. Neither figure for it nor assign to it a nucleus of its own, although Nelson in one place says, "There seems to be some evidence of a yolk nucleus, which is presumably the relic of one of the pronuclear astrospheres. It is hoped that the doubtful points will be cleared up by future studies." Its long connection with one of the blastomeres would seem to indicate that it does not itself possess initiative, and the behaviour of this blastomere would suggest that it finds the yolk a burden.

Another point for consideration is the direction of the first cleavage planes. Korschelt and Heider (1900) give diagrams (Part IV, fig. 11. My Plate V, fig. 16) illustrating cleavage in Lamellibranchs as, first, horizontal, forming a micromere above and a macromere below; second, vertical, dividing the micromere; third, a micromere is obliquely separated above from the macromere, which from the first has had a nucleus of its own. The first cleavage as figured by Horst (1884, Plate I, fig. 3), if he purposely oriented it transversely (Plate V, fig. 17), agrees with this, but Nelson (1901, fig. 80) represents the first cleavage as vertical (similarly to my fig. 11).

A question of some interest, and possibly correlated with both of the preceding, is how far gravitation can affect segmentation. There is a polarity in the distribution of the protoplasm and the yolk, the more pure protoplasm being at the animal pole and the heavier yolk-laden protoplasm at the vegetative pole; the first activity and the polar bodies appear above; the oösperm lengthens vertically before dividing; the nuclear spindles and planes of cleavage, at least for the first few times, have a simple relation to the direction of the chief axis, in that they are either parallel or transverse to it. It seems scarcely possible that such a constant and considerable force as gravitation could fail to have an influence. On the other hand the internal forces of the oösperm are stronger, at least during the time of their activity. Oösperms floating in the water or resting on a solid surface may be spherical instead of deep or flattened; unfertilized eggs fresh from the ovary are usually elongated in the principal axis, although that axis is not vertical for all or even a large proportion of them while in the ovary. In this latter case the eggs are more immediately influenced by their relation to the wall of the fol-

licle and by mutual pressure, since in some species akin to the oyster (Anodonta, Unio, Cyclas) they are attached to the wall of the follicle by their micropylar ends, which may be short or long according to position or pressure.

Brooks states that "three planes of cleavage run in towards the centre of the egg from three equidistant points on the periphery." It is intelligible how cleavages that should be successive may, through accumulation of yolk, be so modified as to occur close together; but when we study the statement in connection with the figures, the three nicks that appear on the surface must resolve themselves into but two planes of cleavage in the sense in which these terms are commonly used, viz., one horizontal, the other vertical, and the horizontal one appears first (figs. 10, 11). The normal direction for the first three planes of cleavage in well known eggs of other animals seems to be 1st, meridional; 2nd, meridional, at right angles to the first; 3rd, equatorial, at right angles to the other two; which would make it appear doubtful if the horizontal constriction here is a true cleavage and at the same time look probable that there is only a single true cleavage, viz., the one falling through from the polar bodies.

Two alternatives are presented, depending upon whether the equatorial constriction represents a true fission into upper and lower halves, or whether it results as a combination of gravitation with the first vertical fission. If the first segmentation plane is equatorial (horizontal), then the oyster will fall in with the diagram given by Korschelt and Heider for the class, the first segmentation spindle will be in the principal (vertical) axis, and one of the daughter nuclei must be hidden in the mass of deutoplasm, which will represent a true blastomere (macromere). Moreover, the first spindle as figured by Nelson and by Brooks (1905) will be not the first but the second segmentation spindle. The diagram referred to does not show a polar body which should be expected at the apex of the micromere. A figure by Horst (his fig. 3; my plate V, fig. 17) does show a polar body, but it is on the side, at the plane of cleavage, where it does not agree with his fig. 2.

If on the other hand the first segmentation plane is meridional (vertical) and fission only partial, not dividing the deutoplasm, the first segmentation spindle will be transverse; each daughter nucleus goes into one of the blastomeres, the deutomere is without nucleus and is not a true blastomere, and the first spindle figured by Nelson and by Brooks is really the first segmentation spindle. This view would bring the oyster oösperm into unison with the great number of others, in that the first two cleavage planes fall at the polar body and are constant for both holoblastic and meroblastic eggs, i.e. for those that have comparatively little yolk deposited in the protoplasm, so that the whole egg can divide into equal halves, as well as for those that have such a large deposit of yolk that the active protoplasm and first attempts at segmentation are confined to a small part of the surface. The oyster oösperm would stand between the two extremes, nearer the first, and present many irregularities. The first fission is only partial and the two blastomeres are not quite equal. The larger retains connection with the yolk and seems to absorb some of it, while at the resting period it becomes completely confluent with it, forming a macromere (Nelson) with a single nucleus in the formative end (Brooks, Nelson). Horst's fig. 3 turned over and rotated until the polar body comes upward, will agree with Brooks' fig. 14. The free blastomere (micromere) then looks like a bud. But the second fission (Brooks' fig. 16) has every appearance of being as normal as the first, dividing both of the original blastomeres vertically at right angles to their first separation—one of the new ones again retaining connection with the yolk.

The egg, the oösperm, and the early stages of the first cleavage are radially symmetrical about the chief (vertical) axis, but the later stages show a bilateral symmetry. The early appearance of this feature is doubtless due to the deutomere, which always retains more complete connection with one of the blastomeres, so as to appear shifted slightly to one side from the axis. What we might call the plane of symmetry would fall through both blastomeres, as well as the deutomere, i.e. where the second cleavage arises. But after the second cleavage is completed the only plane of strictly bilateral symmetry would fall through the deutomere, the blastomere more immediately above it, and the middle one of the other three, while two other blastomeres of different origins lie one on each side. The plane of symmetry is now a different plane from the original one, and in like manner it would shift with each succeeding cleavage. It can hardly be claimed that the bilateral symmetry of this period is strictly comparable with that of the adult, since it is too variable and temporary, radial symmetry predominating again during later periods (morula, blastula, gastrula).

All the foregoing features of the segmentation of the oyster's oösperm can be in a measure understood by considering that the smallest and simplest eggs possess an heredity of structure and of activity, that they are subject to the physical and chemical laws of matter as well as the biological, and that the oyster's egg is further complicated by the deposition of a large amount of food yolk for an egg of its size. This diminishes

the proportion of active protoplasm, and, as gravitation adds weight and pressure, tends to sag into the lower portions and give an equipoise to the floating oösperm. The pure, soft, active protoplasm above flattens across the top and forms a transverse spindle, resulting in an attempt at vertical fission, the only way of effecting an equal division without separating the more active protoplasm from the yolk. The horizontal constriction results from the downward gravitation of the heavier, stiffer yolk below, combined with the upward buoyancy, flattening, division, and rounding up of blastomeres above. The first segmentation nucleus divides into two daughter nuclei that go into the two blastomeres, leaving the deutomere for an interval without nucleus. This does not become independent, but remains under control of one blastomere and its nucleus, as shown in the complete re-union during the resting stage when the segmenting forces are relaxed, and in the fluidizing and absorption of some of the yolk. The second fission follows the same impulses as the first, each daughter nucleus dividing into two grand-daughter nuclei, one for each of the four blastomeres, the yolk still remaining dependent. The later formed blastomeres may be more hampered by their greater proportion of yolk, the earlier formed ones precede them in division, which contributes along with the deutomere to the apparent bilateral symmetry. Similar phenomena in segmentation are shown by *Cardium pygmæum*, *Anodon piscinalis*, and *Nassa mutabilis*.

Having arrived at the termination of embryonic life, we are in a position to better understand the fate of the yolk. In the restricted sense the term yolk includes the whole collection of granules of concentrated food-matter suspended in the egg protoplasm. It is itself passive, and in fact somewhat in the way of any activity on the part of the protoplasm lying around and between the granules. Both together are spoken of as deutoplasm, and occupy the nutritive hemisphere, which in the first cleavage becomes largely separated from the blastomeres as a deutomere. The blastomeres of the earlier stages (or their products by cleavage) become the ectoderm of later stages. The deutomere (or the remnant of it) becomes endoderm. There arises the question as to whether the original blastomeres, by division, give rise to the whole of the ectoderm, thinning out and stretching around the undivided deutomere. This can not be, for the deutoplasm is at first a large mass and later becomes relatively small. Then comes the question of how the reduction takes place. It might occur through absorption into some of the actively dividing blastomeres, which could only be to a limited extent, since it would have to pass by way of that one which remains in contact. Besides, towards the end of segmentation the reduced deutomere itself divides to form the endoderm, but where does its nucleus come from? If the diagram by Korschelt and Heider were to hold good for the oyster the explanation would be forth-coming that one of the first daughter nuclei has remained quiescent all this time, while the other has been active. It is hardly likely that such a thing would happen, or that the nucleus would remain unobserved. Moreover, that the diagram does hold good is improbable. There remains the possibility that the blastomere which retains connection with the deutomere, keeps parcelling out deutoplasm to each new blastomere, formed by division of itself, until it finally merges with the reduced deutomere and effects an equal division. In other words, from the very first fission, the deutomere and one blastomere together form a macromere with one nucleus. The blastomere partially separates from the deutomere, divides off a free blastomere and again merges with the deutomere to form a macromere. All of the free blastomeres are micromeres and continue to segment to form the ectoderm. The deutomere becomes reduced until, at the final merging with the attached blastomere, the nucleus of the latter gains complete control of the reduced deutoplasm, and is able to effect an equal division to begin the mesoderm. This finds a nucleus for every cell and explains all the phenomena, the polarity, the influence of the yolk, the irregularity of the cleavage and in the embryonic stages, the peculiar behaviour of one blastomere and of the deutomere, the fluidization of the central protoplasm of the latter, the position of the nuclei, the alternation of active and resting periods, the increase in volume and number of the micromeres, the reduction in mass of the macromere, the distribution of yolk and its gradual conversion into protoplasm, the late origin of the endoderm, the formation of the gastrula by epibole.

V

LARVAL OR SWIMMING STAGES

A Well Marked Change of State.—In following the development of the oösperm an observer is not met with any remarkably sudden change in structure. Everything depends upon a regular and gradual process of proliferation of cells, a simple, methodical arrangement of these, and a slow, orderly modification to better fit them for their function. The egg, oösperm, segmentation stages, morula, blastula, gastrula pass by such easy and natural transition from one state to the next that it requires close scrutiny to detect in what the difference lies.

But when the hitherto quiescent organism changes its habit and begins to perform automatic swimming movements the phenomenon is sufficiently striking to furnish an easily recognizable and useful mark of distinction between embryonic and larval stages. It denotes the period in time, as well as the condition of structure and activity, when to most people the organism becomes a living animal. There are in the developmental life of the oyster only three such clear-cut, radical changes of state —(1) the egg, the smallest, and simplest, free, but non-motile, stage, which springs, as far as all outward appearances are concerned, abruptly from the largest and most completely organized of all the stages, viz., from the fixed, adult mother-oyster; (2) the larva, distinguished as we have just seen by the beginning of locomotion; (3) the spat, even more remarkable in its sudden precipitation out of the water and fixation upon some solid submerged object.

The larva is the developing oyster during the whole period of the oyster's free-swimming life. It begins with the simple cellular structure of the gastrula and advances until the rudiments of most, if not all, of the tissues and organs of the oyster are originated and brought to some degree of efficiency. It swims about, takes in and digests food, grows, and is sensitive to surrounding conditions.

The Shell-less Larva.—The age at which swimming begins may be considered to be about five hours, reckoned from fertilization, but is subject to variation, depending upon a number of factors, chief of which is temperature. At Shediac (east coast of New Brunswick), July 7, 1909, I put together eggs and sperms of three females and two males in beakers at 10:30 a.m. and at 7:30 p.m. there were plenty of swimming larva. The the temperature of the sea was 17.5° C. (=63.5°F.) and the salinity 1.020. At Bay du Vin (southern portion of Miramichi bay), Aug. 5, a similar experiment just before 12 (noon) gave an abundance of swimming larvæ at

4:45 p.m., temperature 20.5° C. (=68.9°F.) and salinity 1.015. Many such fertilization and culture experiments were performed at Shediac, Bay du Vin, Caraquet (southern portion of Chaleur bay), and Malpeque (Richmond bay, P.E.I.), between June 26 and September 3. It should not be inferred that the difference in time of development to the same point in the two cases given was due entirely to the difference in temperature at these two periods, and not at all to the difference in salinity. Besides an individuality in the oysters and their early or late ripening, a consideration of importance arises from the artificial method. In neither case were the eggs spawned by a natural impulse on the part of the oysters, which leaves a greater chance that they were not equally mature to begin with. Brooks mentions various times (2, 2½, 2 to 4, 6, 11¼ hrs., etc.) and so does Nelson, for the development to the swimming stage.

The size of the youngest swimming larva (Plate I, fig. 9) is about .062 x .055 mm. (Oc. 5, obj. 4 = 9 x 8 = 9 x 6.9 μ and 8 x 6.9 μ.) in length and depth.

The first swimming movement is due to the activity of cilia, developed on the outer surface of the ectoderm cells. These little hair-like processes flap energetically in one direction and too rapidly to be observed except in specimens that are injured or dying. At this period the larva is inclined to be rather broader at one end than the other, the broader end being the one at which the polar bodies are situated, if they have not already dropped off. The cilia at this end soon become larger and longer than the rest and stand on the deep cells of a projecting disk, together forming a definite swimming organ, the trochal disk or *prototroch*, and this stage of the larva is called a trochophore (trochosphere).

Concurrently with the changes in form and surface, the development of a special organ of locomotion, and the definite marking out of the anterior end of the larva, there is a corresponding process in the invaginated endoderm. This will ultimately give rise to the epithelium of the intestinal system and its appended organs, but, due to the mode of origin of the endoderm, it is continuous at the edge of the blastopore with the ectoderm, which contributes in forming the mouth parts.

Behind the archenteron (Plate V, fig. 21), in the angle of the blastocœle posterior to the blastopore, there originates what is to become a third layer of cells, the mesoderm (mesoblast), destined to form the greater bulk of the soft parts of the animal, the muscular and connective tissues, heart, blood, lymph, and other organs. It seems to spring more from the endoderm than from the ectoderm, although at the line of contact between the two, and to spread throughout the blastocœle, lining the ectoderm and coating the endoderm. Exact, conclusive observations of its origin for the oyster are lacking, but the posterior small cells of the endoderm in Brooks' fig. 30 may be homologous with the mesoderm cells in Horst's figs.

10, 12, 13, which correspond with the figures by Hatschek for Teredo, by Goette and by Schierholz for Anodonta, and by Ziegler for Cyclas.

An organ upon the origin of which renewed observation should be made in the American oyster is the *shell-gland*. Brooks described the shell-valves as being formed apart, at the ends of a crescent-shaped transverse groove (his fig. 36; my Plate V, fig. 24), which is prolonged (deepened) at its centre into the primitive digestive cavity at the blastopore. Shortly afterwards Horst discovered in the European oyster that there is a second invaginated depression of the ectoderm (his fig. 8; my fig. 20), distinct from, smaller and more temporary than that of the blastopore, situated on the opposite side, near the original animal pole. He expressed the opinion that what Brooks had taken for the blastopore was nothing but the opening of this preconchylian gland.

That Brooks made some mistake is certain, not only from his association of the shell-valves with the blastopore, but from his location of the permanent mouth, and his orientation of the larva with respect to dorsi-ventrality. His careful continuous observations on the younger stages preclude the probability of his misunderstanding the blastopore and its origin. It is evident from the lack of reference to it, that what he did not comprehend was the shell-gland, which originates about the time of closure of the blastopore. Taking into account the difficulty of turning without damaging the young larva in a microscopic preparation, so as to see the surface of the same specimen from all directions, the depression of the shell-gland might easily be overlooked or mistaken for the blastopore.

According to Horst, the shell-gland originates (Plate V, figs. 20, 21) as a distinct depression, a slight invagination of the ectoderm cells, on the upper surface, just behind the dorsal pole, and opening across the long axis. It deepens, its cells become high and cylindrical, its mouth narrows. Later it loses its original character as an invagination, and forms an ectodermic thickening that secretes a thin cuticular membrane, the first indication of the shell. Carbonate of lime is not deposited in it until later. He agreed with Davaine that the hinge-region is first produced and that the shell originates as a single piece, contrary to Lacaze-Duthiers and Brooks, who believed that the two valves are at first separate. Horst also remarks that "the ectodermic cells, which are found on the surface of the shell, have become very thin and transparent, so that the outlines can not be distinguisded, but only the refringent nuclei." This is a remark difficult to understand and to correlate with his statement about "an ectodermic thickening that secretes a thin cuticular membrane," for how could cells be found on the surface of a cuticular membrane or shell? It must be remembered that older embryologists were frequently content with few, isolated, disconnected observations, and that, therefore, summary statements that are placed together may refer to stages that, in an extensive series of continuous observations, would be separated. It seems possible that the case where the shell-gland "loses its original character of an invagination and forms an ectodermic thickening" was one of evagination of the shell-gland, if not an abnormality. In any case it raises the question of whether the shell is formed as an overflow of fluid secretion on to the surface or as a secretion into a cavity under ectoderm cells, whether as a secretion from cells, a cuticularization of the exposed ends of cells or a transformation of cells themselves. There is a mass of detail yet to be made out with regard to the exact process, the formation of the hinge as distinct from the shell, the origin of the calcareous deposit, the position and serial relationships of the glands that later secrete the different layers of the shell.

My own observations were at first too much taken up with obtaining a balanced perspective of the various stages of development to permit leisure for such special problems—indeed I was not aware at the time of this particular case. It must be understood that the period of oyster propagation is a somewhat brief period for each year, and that there are

great numbers of questions crowding upon the investigator for solution at that time, as well as that mechanical and other operations on the sea or on oyster beds restrict the actual opportunities for microscopic work to few occasions. During the summer of 1911 I had a few limited opportunities to turn to these questions, and I now think that it is possible to correlate most of the preceding observations by supposing that, in the narrowing of the mouth of the gland, a union of anterior and posterior lips is effected along the dorsal line, where the hinge is formed, and that the original single invagination becomes separated into right and left halves, receiving and moulding the glistening irregular drops of semi-fluid secretion that harden into the first minute shell-valves. These thin out, broaden, and take definite shape, covering more and more of the dorsal and lateral surfaces of the larva, and remaining very transparent and inconspicuous above an underlying refractive granular mass. The outer walls of these sacs are above the little shell-valves, and constitute an epithelial layer (the ectodermic cells referred to by Horst) that thins out, ruptures, and continues for some time to double round the growing edges of the shell.

Absence of movement of one part upon another at this period makes it impossible to obtain clear views of the limits of some of the organs. This is especially true of the *mantle*, which must originate out of the layer of cells that form a bed for the shell, and the two doubtless keep pace in growth, yet the mantle can not be distinguished until a later period, when its edges become free from the body.

By this time the *archenteron* has made distinct progress. The original simple invagination deepened and became constricted at its mouth, where growth of ectoderm was directed inwards, pushing the endoderm before it and closing up the blastopore. This in-tucked ectoderm is the primitive stomodæum, and becomes the epithelial lining of the permanent mouth and œsophagus. The archenteron becomes the mesenteron or stomach and intestine, the latter formed as a funnel-like outgrowth backwards from the former and meeting the ectoderm at a new point below the posterior edge of the small shell to form the anus. In-tucking of ectoderm also takes place here, producing a proctodæum, which becomes the rectum.

This account of the origin of the permanent mouth differs markedly from that originally given by Brooks for the American oyster. He believed that the blastopore is formed on the dorsal surface and becomes completely closed over by ectoderm, that a new mouth is formed by invagination of the opposite side, and that the larva has to be inverted for comparison with the adult. On page 23 of his 1880 work he wrote, "The embryo shown in figures 32 and 36 are represented with the dorsal surface below, in order to facilitate comparison with the adult, but in figure 37, and most of the following figures the dorsal surface is uppermost, for more ready comparison with the adult." His figures 32, 36, 37 are reproduced in my Plate V, figs. 22, 24, 25, These views rest chiefly on the one point of the origin of the shell, for this would determine which is the dorsal surface.

The anterior end is first manifested by the earliest swimming movements of the larva; it is the end which precedes in locomotion, the end which bears the prototroch. The opposite or posterior end is often somewhat narrow, but not necessarily pointed or bent. I do not believe the shape is sufficiently set and constant to mark out what is dorsal or ventral, left or right. It requires a great deal of preliminary observation on numerous specimens to decide what form is normal and what is not, for there are many deformities. It seems to me that at this period a normal type is almost symmetrical about the longitudinal axis, which extends from the centre of the prototroch to the posterior end. Organs on the longitudinal axis can not serve to determine the dorsal or ventral surface, but those like the blastopore or shell can, since they occur on but one surface.

It is usual and natural to regard the surface upon which the blastopore opens as being ventral, and with that the other surfaces become fixed. Brooks believed that the shell originates on the same side as the blastopore, and, as the shell is undoubtedly dorsal, then the blastopore must be dorsal. In assigning the shell to the side of the blastopore there is no doubt that he made a mistake, and it very likely came about through his not being aware that a shell-gland is formed by invagination, similarly, but on a smaller scale, to the archenteron. In the larva at the stage of his figure 32 he knew the blastopore, but did not recognize the depression opposite to it as possibly the beginning of the shell-gland. His fig. 36, which exhibits the first appearance of the shell, he of course oriented by comparison with fig. 32, taking the transverse depression to be the same as *g*, whereas it is most probably the same as the depression on the other side, i.e., the shell-gland. The blastopore in fig. 36 being closed, as he believed, can easily have lost its transverse furrow, while the shell-gland was at its best (compare Horst's fig. 11). The ends of the two transverse furrows (blastopore and shell-gland) approach towards the same point on both sides (Brooks' fig. 32; Horst's figs. 11, 12), so that the minute separate valves might easily have been judged connected with the wrong groove. That this is Brooks' own more modern view is shown by his work of 1905, Plate IV, fig. 7, where he reproduces fig. 32 (or one like it turned end for end) and marks *g* of the original as *St* in the new, and the figured but un-named depression opposite *g* is now designated *Sg*.

Horst says: "If one, however, compares fig. 32 of his work with my figs. 9, 10, and 12, I believe that it must be admitted as highly probable, that what Brooks has taken for the blastopore is nothing but the opening of the preconchylian gland." Brooks did not know this gland, Horst did, and yet Horst thinks that *g* in fig. 32 is the shell-gland. Now fig. 33 (reproduced in my fig. 23) is an optical section of fig. 32, and if *g* is the preconchylian gland instead of the gastrula-mouth then where is the archenteron, which ontogenetically as well as phylogenetically should precede the preconchylian gland and would in this stage be present with it? (The condition in the peculiarly specialized fresh-water Unionidæ, where the large shell-gland develops before the small cœlenteron, is doubtless secondary and does not hold for the more primitive marine Lamellibranchia).

We have to consider illustrations as well as statements. When the former are pictures of actual natural objects they are more likely to be trustworthy than the latter, but when they are merely diagrams to illustrate the thoughts they are just as likely to be modified by theory. Fig. 32 is the picture of a natural object; whether it was a fortunate selection from among millions is open to question. Fig. 33 may be partly diagrammatic, illustrating what the author believed he saw, but both possible and probable. Brooks believed *g* to be the blastopore and that the shell-valves originated in relation to it. He did not discuss the depression opposite to it, but, if he thought about it at all, may have considered it the beginning of the future mouth. Horst, in interpreting the figure, believed that *g* was the shell-gland, and did not discuss the position of the blastopore or of the future mouth, but may have considered them to be represented in the opposite depression. If so, fig. 33 proves that it cannot be the blastopore since it is not connected with an archenteron, and similarly it is not the future mouth as there is no enclosed archenteron into which it can open.

My own view is that Brooks' figures are correct representations of the object, but that both he and Horst misinterpreted them in that both thought the shell originated at *g* in figs. 32-35. The whole difficulty seems to turn upon Brooks' fig. 36, which doubtless should be inverted, when it would fall naturally between 32 and 37, and *m* of 37 would be the definitive mouth, in the position of the original blastopore, corresponding to *g* of figs. 32-35, but closed even to the loss of its transverse furrow in 36, where its position would be on the side opposite to the shell and transverse furrow of the shell-gland. This perhaps accounts for the posterior end (anal papilla) being bent in a direction opposite to what it is in the preceding figures. According to this

view, Brooks did not mistake the blastopore, but mistook the place of origin of the shell (and, implicitly, of the shell-gland, although this was unknown to him.)

In the orientation of the larva with respect to the constant direction of gravitation, i.e. the fixation of dorsal and ventral, anterior and posterior, right and left, the organs of earliest and easiest recognition, such as blastopore and prototroch, shell, mouth, and anus, are of first importance, and it is of great advantage to preserve a constant, continuous, and uniform method, such as renders it unnecessary at some particular stage to turn the larva upside down for comparison with the egg on the one hand or the adult oyster on the other. This is what Brooks did at the stage of his fig. 37 (1880 but not 1905), and what Nelson did at fig. 7 (1902). It requires some rearrangement of this part of their works, in the light of Horst's observations (1884), to make a logical presentation.

With the first appearance of the prototroch it becomes clear which is the anterior end. With the first appearance of the shell it is plain what is the dorsal surface. It is then evident that the blastopore (as well as the permanent mouth) is ventral, and that it is possible to return and, in a general way, to fix directions from the very first cleavage. Even before this, dorsal and ventral may be marked out by the position of the polar bodies and active protoplasm above, and of the deutoplasm below, but for the rest there is radial symmetry about the chief (vertical) axis. The first fission is transversely vertical, resulting in an incomplete anterior blastomere (united with the deutomere to form a macromere) and a more complete posterior blastomere (micromere). The symmetry is radial with two rays, giving it the appearance of being bilateral—the two rays being necessitated by the process of division. The second fission is longitudinally vertical, but it is scarcely justifiable to claim that two blastomeres are anterior and two posterior. The deutomere adjusts itself more particularly to one of these, which, if bilateral symmetry predominates, must be the anterior one, leaving the other three respectively posterior, right and left. This shifting of the plane of bilateral symmetry shows that the latter is not yet established. Radial symmetry (here with four rays) exists, and continues (with increasing number of rays) to exist throughout the process of segmentation, up to the completion of the gastrula. During this time the area of most activity changes from dorsal to posterior, then anterior, and finally ventral; and there are alternations of apparent bilateral with radial symmetry. Radial symmetry is characteristic of the egg, oösperm, and embryo, during their floating and resting conditions; bilateral symmetry first becomes prominent with the free-swimming larva. It would seem that gravitation first determines dorsi-ventrality, and with it horizontal radial symmetry, which becomes more emphatic with growth along compass lines of equal pressure, and tends to be sustained by habits of rest, flotation, fixation; and that automatic locomotion through a resisting medium necessitates especially a monaxial growth of the body, a continual precedence of one end, and an equal balancing of right and left sides, i.e. bilateral symmetry.

In the origin of the permanent mouth from (or in the position of) the blastopore, Teredo, Cardium, Modiolaria, and other genera of Lamellibranchia agree with or approach to Ostrea. This appears also to be the rule among marine Gastropoda (e. g. Patella), Scaphopoda (Dentalium), and Amphineura (Chiton). But according to various earlier observations, there are exceptions or modifications from this, chiefly among fresh-water Unionidæ and Pulmonata, where the blastopore may become the anus (Pisidium, Paludina), or extend as a slit from mouth to anus (Lymnæus, Planorbis) or become closed on the dorsal surface and have no relation to either mouth or anus (Anodon). In the fate of the blastopore, as in segmentation, there appears to be so little unity among genera that are classed together as to make renewed, special, and extensive observations desirable.

The Shell-bearing Larva.—It has been already pointed out that the beginning of swimming locomotion marks a convenient halting-place for stock-taking in organization, and that with regard to the latter the prototroch is the most conspicuous feature. The next most recognizable character to serve as a mile-post in the train of events is the ***shell***. The formation of a shell-gland, and of a shell, furnishes the first distinctive indication of the molluscan origin of the larva, and separates the period of the pre-conchiferous trochophore from that of the conchiferous veliger. The trochophore, or a slight modification of it, is the larval form of several

large groups of animals (Rotifera, Turbellaria, Nemertea, Annelida, Gephyrea, Echinodermata, Bryozoa, Brachiopoda, Mollusca, &c.), but the veliger is peculiar to Mollusca only. A veliger is an advance on a trochophore, not only in the possession of a shell, but also in the conversion of the simple prototroch into a velum, which is a more efficient swimming organ, capable of being folded and withdrawn into the shell for protection. The oyster larva is a veliger from the time of origin of the shell throughout the rest of the oyster's larval or free existence. During this period it grows to more than five times its original length, i.e. more than one hundred and twenty-five times its original cubic contents, and undergoes a corresponding advance in organization, The new organs, being soft cellular structures, are, as a rule, inconspicuous, at least until some time after their origin, so that they are ill-adapted to serve as land-marks in dividing off stages or periods for accuracy of description. For this purpose the shell is the most serviceable, because of its permanence, its regularity in size and shape, and its growth in correspondence with the soft parts.

The shell first becomes recognizable (Plate I, fig. 10) when the larva is about 10 units ($=10 \times 6.9\,\mu = .069$ mm.) in length. As already intimated, the age of the individual is too variable to be of much use in comparisons, varying with a northern or southern climate, a sheltered or exposed locality, depth of water, &c., i.e., with the temperature; but, since an approximation is better than nothing, I will select a single example.

Shediac, N.B., Aug. 2, 1909. Surface sea-water 22.5° C. (=72.5°F.); S. G. 1.018. 11 oysters examined furnished two small ripe females and one male. Eggs and sperms mixed at 10:05 a.m. Kept in sea-water in tumblers aboard the "Ostrea" and at 5:30 p.m. next day, at Bay du Vin, contained larvæ with minute shells.

At first each shell-valve appears as a small glistening spot on the side of the soft-bodied larva, near its dorsal surface. It grows larger, covering more and more of the body (fig. 11), becomes connected with its mate of the opposite side along the hinge-line, and together they extend downwards and increase in length until they can enclose all of the larva except the velum (fig. 12). At this time the shell measures 10 units in length and 8 in depth, with an almost straight hinge-line of 7 units (10 x 8: 7), from the ends of which it curves equally in front and behind. It is narrow from side to side, its two valves are of equal size and shape, concave inwards, convex outwards, thin, gray, and transparent. The larva is very inactive, except when swimming, but twitching movements of the valves and of the velum show the presence of adductor and retractor muscle-fibres. There is an œsophagus and a short intestine, and the liver is forming from the stomach (Plate V, fig. 26).

Up to this time the larva has not increased much in size beyond the original egg, the protoplasm of which has furnished food and energy for

development and activity. From this period onwards it becomes next to impossible to keep specimens alive, which is doubtless principally due to the difficulty of supplying them with suitable food without injuring or losing them.

Rice (1885 p. 116) stated: "The first efforts in this country in the direction of artificial propagation were made by the writer in the summer of 1878 in conjunction with Dr. W. K. Brooks, but these experiments were not successful. The next season, however, Dr. Brooks succeeded in impregnating the eggs and raising the embryos until they were six days old, when they all died for lack of fresh water, as Dr. Brooks was unable to arrange any apparatus which would admit of a current of water through the breeding vessel that would not allow the young oysters to escape."

Brooks (1880 p. 25) wrote: "The stages shown in figures 44 and 45 agree pretty closely with the figures which European embryologists give of the oyster embryo at the time when it escapes from the mantle chamber of its parent. The American oyster reaches this stage in from twenty-four hours to six days after the egg is fertilized .. .. All my attempts to get later stages than these failed, through my inability to find any way to change the water without losing the young oyster, and I am therefore unable to describe the manner in which the swimming embryo becomes converted into the adult, but I hope that this gap will be filled, either by future observations of my own or by those of some other embryologist."

Winslow (1882 p. 757) "Our observations at Beaufort showed us that after the embryos had once developed the shell to any extent there was little motion of translation, the animals remaining quietly in one place at the bottom. Indeed their specific gravity at this period, together with their deficient locomotive powers, should prevent any very rapid or extensive movements .. .. .. the oyster embryo is predisposed at least to fix itself very soon after the process of segmentation is completed."

Horst (1882 p. 165) "Older stages than that represented in fig. 12 I was unfortunately not able to investigate, so that regarding the length of the period which intervenes between the time when the larvæ are set free, and the time at which they fix themselves, as well as the changes which they undergo during this period, I am unable to affirm anything."

Ryder (1882–3 p. 328) "Fig. 1 in the accompanying Plate LXXV, which represents a young American oyster in the larval or fry stage enlarged 250 times" (In the description of the plate he stated "enlarged 183 times.") "The duration of the locomotive stage of development of the larva has not yet been certainly determined for any one of the three species of which the development has been studied."

Huxley (1883 p. 53) "How long the larval oysters remain in this locomotive state under natural conditions, is unknown, but they may certainly retain their activity for a week, as I have kept them myself in a bottle of sea-water, which was neither changed nor aërated for that period."

Horst (1884 p. 904) "The larva represented in fig. 16 is the most advanced stage of free larva which we have observed; this had been taken from the mantle cavity of the mother oyster, or had been ejected by it when placed in an aquarium. I am not able to say anything positive in regard to the duration of the period which elapses from the time when the larvae become free to the time when they become fixed; nor do I know what changes they undergo during this period. ....At first the shell grows very rapidly, for while it only measures 0·16 millimeters in height in a larva which is on the point of leaving the mother oyster, it measures more than 0·24 millimeters in the smallest of the fixed shells."

Ryder (1884 p. 727) "Our experiments made at St. Jerome creek during the past summer gave the most contradictory results, and the interval of development between that of our oldest embryo with its diminutive Pisidium-like valves measuring about 1/500 inch in diameter and that of the embryo when its valves first begin to lose their embryonic form, still remains unbridged. The dimensions of the embryo or fry, as we may more properly call it when it becomes fixed, are between 1/80 and 1/90 inch according as the measurement is made longitudinally or transversely. The difference in magnitude between the oldest artificially incubated fry seen by me and that of the youngest fixed embryo which I collected is very small, amounting only to 41/4500 inch, or a little more than 1/109 inch."

Rice (1885 p. 115) "The attachment takes place in about two days from the time of fertilization."

Jackson (1890 p. 300) "Between the stage fig. 25, and our next stage, Plate XXIV, figs. 1–2, there is a blank in the knowledge of the development of the oyster. It has

not been described in the European species, and all our attempts to obtain it in our own species bave failed. In artificial confinement the oyster dies at this stage."

Nelson (1901 p. 310) "The fry, after about five days, develop a two-valved shell, and then they seek a place to settle down on."

Nelson (1902 p. 333) "These eggs rapidly develop into small, free-swimming fry, that in a few days are provided with a bivalved shell; and then they settle down on a clean surface, of a shell or stone, etc., to which they become attached by the left side."

The foregoing quotations acknowledge that there was a limit to which the development of the oyster had been continuously observed. The figures by Brooks, Horst, Huxley, Ryder, Jackson and Nelson were very near to the young straight-hinge stage I have just described (Plate I, fig. 12; Plate V, fig. 26) and represented the oldest larvæ known. The next stages known were fixed stages (spat), of much larger size and different shape (about the same as my Plate I, fig. 22). Between the two was a period of unknown duration—the 'gap' of Brooks, the 'intervening period' of Horst, the 'locomotive state' of Huxley, the 'unbridged' interval' of Ryder, the 'blank' of Jackson. Brooks was not inclined to speculate beyond the facts of his observations. Winslow believed that the oyster larva was predisposed to fix itself very soon after segmentation. Ryder thought it might do so in 24 hours. Rice mentions 2 days, Nelson 5 days. Huxley had kept larvæ for a week, Rice for 14 days, Lacaze-Duthiers for 30 and even 43 days without apparent change. This behaviour in confinement must be different from what it is in the open water of the sea, but what the latter might be nobody knew.

Plankton.*—This was the condition of the subject when in 1904, I began my work at Malpeque, although at the time I had little knowledge of what had been done or remained to be accomplished. What I undertook was to gain some first-hand practical information about the breeding and embryology of the oyster in one of our own northern oyster areas; and I am sure nobody has been so much surprised as myself that, in the course of one short season, I had the good fortune to determine the time, place and manner of all the important events in the developmental history of our oyster, to add a new chapter to the literature of the subject by filling up the gap referred to by Brooks, the unbridged interval of Ryder, or the blank of Jackson, and, along with my subsequent researches, to furnish abundant data for a clear perspective of the complete ontogeny of the oyster. Important as this is from the standpoint of morphological and theoretic zoology, it is perhaps surpassed in value by the light thrown on economic problems and methods of oyster culture. Artificial methods of breeding oysters in a small way had succeeded, as we have seen, in the hands of a few practical zoologists only in bringing the young to a free-swimming stage of little over .069 mm. (= 1/360 inch),

**Plankton,* a term applied collectively to all those minute animals and plants which swim or float about in any of the great natural bodies of water.

when they would all die off. As long, I suppose, as the oyster has been known to man, it has been known that, under normal conditions, it is attached to some solid body in the sea-water. By tracing back through smaller, younger oysters, fishermen and culturists were able to arrive at comparatively small specimens, perhaps but little smaller than a man's thumb-nail, which, along with all other small sizes, had been called "spat". It was found also that, by placing solid bodies such as stones, shells, bones, tiles, lumber, ropes or other objects in the water near oyster beds, a "set" of spat could sometimes be secured. The spat recognizable by fishermen and others unacquainted and unprovided with microscopic appliances were somewhat large objects, but a few expert zoologists had succeeded in procuring several very young spat. These were at least five times the length and one hundred and twenty-five times the volume of the larvæ reared by artificial fertilization and culture. The intermediate stages were unknown. The character of these stages, the place of occurrence, the time of the year, the length of the period, and the manner of existence were alike unknown. It may have been conjectured that they lie on the bottom or become set to rocks, shells or weeds, or that they float about somewhere in the water. At least these are some of the possibilities that occurred to me and called to mind my former observations on mussel larvæ, as already outlined in the introduction. I accordingly began the first systematic use of the plankton net in the search for oyster larvæ, and it resulted in discovering all the stages between the oldest veligers that had been known and obtained by culture and the youngest natural spat that had been procured on glass, shells, etc., in the sea.

In a brief preliminary account of what I regarded at the time as the most important results of my first summer's work occur the following statements about the larval oyster in its oldest plankton stages:

"We have been accustomed to think of it as vastly different from other bivalve-larvæ, corresponding to the early assumption of a sessile mode of life. This misconception is due to lack of observation of plankton stages, embryologists having jumped from early veliger or phylembryo to late prodissoconch or even early nepionic periods."—(Amer. Nat., Jan. 1905, p. 41).

The plankton was collected in nets made of fine-meshed, silk bolting-cloth, cut and sewed so as to be conical in form, with smooth overturned seams, without unnecessarily exposed needle-holes, and with no folds. To take the wear, a double band of strong linen was used to attach the broad end of the net to a thin but firm iron hoop, one foot in diameter. A similar band strengthened the small end of the net, which was of just sufficient size to slip over the neck of the broad-mouthed bottle and be fastened by tying a string around it. To the hoop were attached three

equally spaced pieces of cod-line, the other ends of which were brought together and secured to the towing-line, to which was suspended a short iron sinker. This apparatus was thrown overboard and dragged behind a row-boat, sail-boat, motor-boat or steam-boat under reduced speed, the depth of the net being regulated by the speed of the boat, the length of the tow-line, and the weight of the sinker.

Water filters through the net, but organisms are kept back, collect on the inside, and tend to be carried into the bottle. This arrangement is rather better than a closed net, where strong filtering currents passing through the point of aggregation of the organisms are liable to damage them. On the other hand the bottle fills with more or less stagnant water, tending to block their entrance to it, but permitting many to fall by their greater weight. Care is necessary, in hauling the net up, to not lose those clinging to its inside. By draining and dipping several times they may be washed down into the bottle, which may then be removed from the net, corked and stood in a pail of cool sea-water in the shade. The net may be cleaned by throwing it out again, open, and a fresh bottle used for a different locality or a different depth on the same excursion.

Bivalve Larvæ of Plankton Collections.—In such a manner may be procured a wealth of plankton material that, when fresh, may at first sight present much of the appearance of pea-soup, but when the bottle is held up to the light it can be seen that each tiny speck is a living, free-swimming or free-moving organism. Being confined in countless numbers in a small quantity of water, they soon begin to die and drop to the bottom; at the same time the mass becomes more pink in colour from a change in the pigment of its numerous little crustacea (copepods), similar to that which occurs when fresh lobsters are thrown into a vat of hot water.

The older stages of bivalve-larvæ are compact, heavy objects, that as soon as they are disturbed cease swimming and sink to the bottom, where, protected by their shells and on account of their hardihood, they will keep alive for hours. They can be seen as a darker, granular, more sandlike layer underneath the great fluffy mass of lighter-coloured, pinkish copepods. They may be drawn off by inserting one end of a glass tube, the other end being closed by the finger, to the bottom of the bottle, when, upon relaxing the finger for an instant, the water will rise rapidly in the tube, carrying some of the bivalve larvæ in the current. If the finger is again pressed upon the top and the tube quickly withdrawn and allowed to drain into a deep watch-glass, what lighter objects happen to have been carried over may be removed from the surface by a pipette, leaving the bivalve-larvæ in thousands almost entirely free from admixture with other animals, and among them, if collected at the right time and place, will occur oyster larvæ.

Younger stages are also obtained in this way, but, on account of their lighter weight, do not so readily make their way to the bottom. Even pre-conchiferous trochophores and segmenting stages may be procured, but in collecting them it becomes necessary to exercise greater care. The high speed and rough usage with which the shell-bearing larvæ may be safely collected might prove completely destructive to the delicate shell-less stages. The method, however, is of no special merit, except as a proof of occurrence, in the study of these young stages, for they can be obtained with greater ease and in vaster numbers by artificial fertilization, and besides the latter has the additional advantage that the parents are already known.

Identification of Oyster and Other Bivalve Larvæ.—Identification for the first time of oyster larvæ in plankton collections was difficult, but, when once determined, at least the older stages could be recognized almost at sight in succeeding catches. Some account is given in the introduction of how this was first accomplished. It scarcely needs stating that the plankton net collects whatever comes in its way, and that therefore oyster larvæ will form but a small part of the total catch. The method I have adopted separates the bivalve larvæ from a great mass of other things, but, even with this done, the bivalve larvæ of themselves represent many species, and it becomes a question how to distinguish the oyster larvæ from the rest.

Larvæ do not look like adults. Those of the same species at distant intervals of time may appear as unlike one another as different species. It is difficult to find a point of departure in distinguishing them. One may begin with the size, the shape or the colour, but after a time find that he cannot trust to impressions and memory. He may recognize differences, and gradually arrive at the conviction that certain of these are constant, but later on find out that there are intermediate conditions. He may notice that certain characters are associated, and have to go over his collections again to decide upon combinations, such as colour and shape, length and depth, and discover that he cannot safely trust to the eye in judging proportions. All of this takes time, but is a clear gain in experience and knowledge, and begins to determine a definite point of view and a consequent mode of procedure. Having reached this point, I started to make new sketches with such arrangement of oculars, objectives, and drawing apparatus that I could obtain accurate outlines of all stages from the smallest to the largest larvæ under exactly the same conditions, and at the same time make use of a definite and unvarying method of measuring by means of ocular and stage micrometers. Loose sheets of paper were used so as to permit of easy re-arrangement; on the right side was placed a table of lengths proceeding by one of the smallest units of the ocular micrometer at a time, while on the left was kept a space for the sketch. Then larvæ were sought out corresponding to these lengths and

the depths filled in and sketches made with a drawing apparatus. After a good number of these had been made, a comparison both of the outlines and of the measurements would indicate whether a given size fell naturally between the preceding and succeeding ones, and consequently whether all members of the series seemed likely to belong to one species. Wherever it was necessary the greatest care was taken in reading measurements, even to the splitting of the micrometer lines and in using the same longitudinal and vertical axes, the larvæ being placed in the position of a creeping clam with the umbos above and the foot below. With ocular V and objective 4, the measurements for the shell of a free-swimming larval mussel, for example, extend all the way from 15 to 58, each unit of which as determined by a stage micrometer representing a value of 6.9 μ. A pretty complete series of this species was formed, which agreed with drawings and measurements I had made of young mussels found attached in the axils of rock-weed (Fucus) at St. Andrews, when I was studying the clam-fishery in 1900.

Having determined the mussel, it served as an excellent guide in pursuit of others, and at the same time simplified matters by eliminating from the field of research the most overwhelmingly abundant of all bivalve larvæ. It was found that the distribution of plankton stages of the mussel corresponded with the distribution of adult mussels, and this suggested a faunistic study of bivalves as a means of determining the most probable larvæ to be expected. At Malpeque, Mytilus, Mya, Ostrea and Venus are all plentiful, while Clidiophora, Anomia, Mactra, Modiola, Pecten, Saxicava, Macoma, Ensis, Yoldia, Cardium, Tottenia, Kellia and others occur in considerable numbers. It was apparent that there were many species of bivalve larvæ in the plankton, but there was nothing in them to directly betray their affinity with the adults, and I had no means of referring them with precision to their proper species. Under such conditions no certain steps of progress could at the time be made by following up the comparison, so I turned to experiment. I set out below low-water mark crocks containing strips of glass held separate by wire networks and in a short time had the satisfaction of finding, fixed to the glass, minute spat stages, in the umbonal regions of which could be recognized the familiar plankton shell I had already suspected to be that of the oyster. New observations came thick and fast. To follow the free-swimming plankton larva of the oyster into the fixed stages of the spat was not enough. It became desirable to discover also what its different companions were, for, by proving that they were the young of other species of bivalves, it would make the case of the oyster more secure. The larva of Anomia was determined in a similar way to that of the oyster. The larva of the clam was kept under surveillance during the following seasons at Gaspe, but was not definitely determined until two years later, when I returned to St. Andrews, the great centre of the clam fishery.

The larvæ of the scallop and of the quahaug were determined by a comparative study of preserved plankton collections from Malpeque, Gaspe and St. Andrews, combined with observations on the distribution of the adults—the scallop with its equal measurements in length and depth corresponding with the prodissoconch of 2 mm. scallops dredged on hydroids in Gaspe bay, and the quahaug occurring in both plankton and dredgings at Malpeque, but not at Gaspe or St. Andrews, and also agreeing with the prodissoconch of small quahaugs 2 or 3 mm. long collected in the sand at Ram Island point, Malpeque.

Of these six species of our commonest bivalve mollusks, of which the larvæ were mostly determined by being traced into succeeding older stages, only that of the mussel was known to me from the straight-hinge period upwards. I now turned to my preserved plankton collections and found that at Malpeque on July 11, 1904, there were swarms of straight-hinge stages varying about 15 units in length. A hasty and superficial examination of these, combined with their occurrence in proximity to oyster beds, might easily have led to the conclusion that they were all oysters. This mistake had been made by others. But they are not all oysters. A few are readily identified as mussels, the rest look different and may be presumed to be oysters. Upon measuring them with great care it is found that they are deeper in proportion to their length than the mussels, but that, besides, some of them appear rounder than others, due to their having a shorter hinge-line. There are in reality two different species of deep ones. Gaspe and St. Andrews plankton was re-examined, and it was found that those with the shortest hinge-line do not occur at these places, but that the other deep ones do. At once it was suggested that the former are oysters and the latter clams, corresponding with the distribution of adults. Selecting examples of exactly the same length the dimensions are:

	Length	Height	Hinge
Mussel	15	10	11
Clam	15	13	10
Oyster	15	13	7.5

The eye can easily perceive a difference in the proportions of a mussel as compared with a clam, but it requires a certain refinement of judgment to do the same for a clam and an oyster. Faithful selection, examination and measurements have filled up the intervals between these small straight-hinge larvæ and the large umbo-stages sufficiently to satisfy me that these observations are correct. Moreover, I have since pursued the subject backwards to smaller plankton stages and find it holds good.

Adults are easily distinguished; the full-grown larvæ less easily, for, since they bear little resemblance to the corresponding adults, other marks of distinction have to be selected; but the young larvæ are still more diffi-

cult, for, according to the biogenetic law, the younger they are the more nearly they resemble some stage of the common original ancestor, and of course approach one another in likeness. Under such conditions the practicable, distinguishable characters may again be different and require a more critical scrutiny. The generic characters which distinguish a full-grown mussel, clam, or oyster do not hold good for the umbo-larvæ of these species, and the most striking features of the umbo-stages in their turn have to be relinquished when we come to consider the straight-hinge larvæ.

Time of Occurrence of Oyster Larvæ in Plankton.—Having reached the point when the youngest shell-stages of the oyster larva, raised from artificially fertilized eggs by Brooks, Rice, Ryder, Nelson, myself, and perhaps by others, could not any longer be kept alive and growing, and their further development could not be followed; and having determined when, where, and how the succeeding stages may be procured and identified; we may now return to their description in the order of size and age, following from the largest described and figured by Brooks.

In 1904 it was not until the fourth week of July that my observations became sufficiently advanced to permit a conjecture as to what particular larva was the young of the oyster. Fortunately I had preserved samples of the plankton at short intervals from July 8th, which I could re-examine after I had learned to distinguish the oyster. In this material (preserved in formalin or in alcohol) oyster larvæ first occur on July 11th, and ranging from 12 to 20 units in length.

In 1905 I had kept samples between June 7th and 26th, and on the latter date there were a few oyster larvæ 14, 15, and 16 units in length. This is the earliest record I have of oyster larvæ in the plankton. Putting the two years together, these samples range from June 7th to Sept. 19th.

In 1909 I preserved plankton every two or three days between June 25th and September 3rd, taken at Caraquet, Shippigan, Bay du Vin, Richibucto, Buctouche, Cocagne, Shediac and Point du Chêne, on the east coast of New Brunswick, and at Charlottetown, Summerside, Cascumpeque, Bideford, Grand river, the "Upper bay," Richmond bay and Malpeque bay, in Prince Edward Island. Besides the occasions on which I kept preservations, I examined fresh material almost every day, and sometimes from several localities on the same day. In this year I was prepared from the first to recognize, almost at sight, any stage of an oyster larva, so that the observations made are quite correct for the locality and season. I am satisfied, however, that the season was exceptionally late (about three weeks later than usual), and not only for marine faunas and floras, but it was a subject of concern to fishermen and farmers alike. Minute oyster larvæ, of which the shell measured 10 x 8:7, were first observed in fresh material at Cocagne on July 22nd, but later careful search through the preserved material showed an occasional specimen on July

12th, at Richibucto. Full grown larvæ of 55 x 50 occured first at Bay du Vin on Aug. 5th, from which it may be understood that the free-swimming life of the larva continues for at least two weeks after it has reached the shell-bearing stage.

Literature on the Larva

Brach (1690), who was perhaps first to use the microscope in the study of the young of oysters, distinguished two stages of development within the shell of the mother (of the European oyster): (1) white, somewhat spherical, quiescent eggs, and (2) white, round, compressed eggs with valves and spiral movement (evidently what we would now call larvæ).

Leeuwenhoek (1695) observed young oysters (also taken from the parent), that moved about rapidly in the water by means of small organs projecting from their shells and which they drew in when they died (the velum).

Davaine, Lacaze-Duthiers, Coste, de la Blanchère, Gwyn Jeffreys, Saunders, Salensky, Möbius, Horst and Huxley all observed the larva of the European oyster, taken from the parent.

Huxley (1883) states: "During the summer and autumn months, from as early as May to as late as, or even later than, September, according to circumstances and the depth of the water in which the oysters live, which appear to be most influential, a certain proportion of the oysters in an oyster-bed pass into a peculiar condition, and are said by the fishermen to be 'sick.' In about half of these sick oysters a whitish substance made up of innumerable very minute granules, embedded in and held together by a sort of slime, collects in the infra-branchial chamber, filling up the interspaces between the mouth and the gills, and between the gill-plates themselves, and even occupying the vestibular cavity so completely that it is difficult to understand how the processes of breathing and feeding can be carried on.

"This granular slime is what is known as 'white spat' and the granules are the eggs of the oyster. By degrees the granules become more or less coloured; and the mass acquiring a brownish hue, is termed 'black spat'. This change depends upon the development of the young, which acquire a certain degree of coloration, within the eggs. At the end of a period, the length of which varies with the temperature of the water and other conditions, but appears rarely to exceed a fortnight, the mass of black spat breaks up, and the young, hatched out of the eggs, leave the mantle cavity of the parent in which they have been thus incubated. They become diffused through the water and swarm in vast multitudes at the surface of the sea.

"A single full-grown oyster produces, on an average, about a million of these free-swimming young or larvæ. If a glass vessel is filled with the stratum of surface water, in which the larvæ swim, and held up to the light, it will appear full of minute particles—only 1/150th of an inch long, and therefore just visible to the naked eye—which are in active motion."

Huxley gives a good diagrammatic figure (his Fig. 3) of a straight-hinge larva.

Horst (quoted from on pages 27, 30), whose earlier work preceded and later work followed that of Huxley, also figures a young straight-hinge stage, and both his and Huxley's measurements agree with the earlier statement of Möbius (1887) that "the young oysters leave the mother when they have reached a size of 0·15 to 0·18 millimeter."

In America the method of procuring young developing stages, extending from naturally fertilized eggs to straight-hinge larvæ, as practised upon the European parent oyster, is not possible. On this account another method, that of artificial fertilization and culture, has been developed by Brooks, Ryder, Winslow, Rice, Nelson and others. The earlier references to this method are all too brief and scattered. Its possibility on a small scale is an embryological feat of great interest and importance. It is an easy matter to raise up larvæ to the corresponding stage of structure known to European embryologists.

Brooks has been already referred to (pp. 3, 21, 24 et seq., and 30).

Ryder's papers are not easy to correlate on account of little discrepancies in measurements or magnifications, age and occurrence, a variable use of the terms embryo, larva, etc., and involved or ambiguous statement. They all seem to depend upon his experiments, along with Colonel McDonald, at St. Jerome creek, Maryland, June 24, 1882, (1882, p. 383). "The most remarkable result obtained was the apparent fixation of the fry to the sides of the glass hatching vessels twenty-four hours after impregnation."

The temperature was 72° to 80° F. The fry (young straight-hinge larvæ) remained of about the size of the eggs put into the hatching apparatus, containing filtered sea-water, and did not grow any during the three days under observation. He did not know how they were attached, but they lay upon the side or in other positions, with the border of the mantle projecting over the edge of the shell, and could not be washed away by a stream of water. They could only partially retract velum and mantle. The shell was perfectly symmetrical; hinge-line straight, without umbos. The adhesive organ was probably the border of the mantle, although an unobservable temporary byssus may have existed. Attempts to repeat the experiment failed. His Fig. 1 ("Young American oyster two days old, magnified 183 times") measures 14·5 mm. as length of shell, which, when reduced to the actual length (14·5 ÷ 183) gives ·08 mm., somewhat larger than an egg, but near enough to justify his statements. This agrees closely with the figures 42 and 44 by Brooks, and to one familiar with the subject can be recognized as of approximately the same stage, notwithstanding the absence of measurements from Brooks' work. It is evident that the age (two days in one case, and twenty-four hours to six days in the other) can not be depended on in making comparisons, and the larvæ observed by Ryder would have measured the same at the end of five or any other number of days as at the end of two, since they did not grow. Hence the necessity of taking account of measurements and organization.

For a reference to Ryder's 1882–3 paper, see p. 30.

At the same place, in August of the same year, Ryder obtained young stages of spat, of which the youngest was his Fig. 3, magnified 96 times. The figure measures 29 mm., which gives an actual length of ·3 mm. (sufficiently correct).

For a quotation from his 1884 paper, see p. 30.

Ryder, we conclude, had two stages, represented by his Fig. 1 and Fig. 3, both attached, and in fact it was due to their attachment that, with his methods, he was able to find them. The younger agreed in size, age and appearance with straight-hinge larvæ, raised by culture; in reality these were so obtained. The older, on the other hand, agreed in size and appearance with young spat that had "only just begun to develop the spat shell." He could not correlate the two stages of attachment except on the supposition that "under favourable circumstances attachment of the fry probably takes place within twenty-four hours after fertilization . . . . The young, however, after attachment continue to grow as larvæ . . . . When the valves of the fry have acquired umbos the development of the spat shell begins." We know now that Fig. 1 represented an abnormal attachment, most likely due to unfavourable (rather than 'favourable') artificial conditions. Ryder was confined to a single observation and he did not know that there were in the open waters of the sea, perhaps at the very moment, incalculable millions of free-swimming umbo-stages that would bridge the interval of development between his two fixed stages. He was himself suspicious that the youngest were not normally attached for he remarks: "Our conclusion was that these young embryos had voluntarily attached themselves . . . . this young fry had a disposition to lie upon the side . . . . Many were noticed in other positions, but I am inclined to believe that these were not normal." He should also have noticed that the one he selected to draw was not normal, in that it was attached by its right side instead of the left. Jackson (1890, p. 300) referring to this very case of Ryder's stated: "From my own observations I have every reason to believe that the fixation was of a transitory nature." Attachment at this size is certainly exceptional and unnatural and these were certainly not normally attached by the shell but likely clung by the protruded edge of the velum or mantle. Yet the single observation of this abnormal case influenced Ryder's views to the extent that we must continually keep it in mind in trying to understand his statements. If this fixation were regular then the period of free larval life preceding it must have been very brief, for fertilized eggs had been raised to this stage and the period was approximately known. Hence the statement that, "The difference in magnitude between the oldest artificially incubated fry seen by me and that of the youngest fixed embryos which I collected is very small." The "youngest fixed embryos" here referred to were those of Fig. 1, not Fig. 3. On the other hand the period and the animal (whether free or fixed) between stages 1 and 3 were completely unknown: "The interval of development between that of our oldest embryo with its diminutive Pisidium-like valves measuring about 1/500 inch in diameter, and that of the embryo when its valves first begin to lose their embryonic form, still remains unbridged." The first refers to Fig. 1, the last to Fig. 3. He was primarily interested in determining the mode of fixation of the larva, but secondarily in estimating the period of free existence by discovering the youngest stage of fixation. "The attachment is effected very early, as I have met with it in spat a little over an eightieth of an inch in diameter." This refers to Fig. 3, not Fig. 1.

Combining the statements of his various works in this way, Ryder's views may appear self-evident, but let a reader, unfamiliar with the true history of development of the oyster, try to understand his papers separately and I doubt if he can make much headway. One of the greatest causes for ambiguity arises from the varying meaning of terms, in which Ryder is not the only one to err. "Embryo" may refer to either "embryo", "larva" or "spat." "Larva" may mean either "larva" or "spat." Ryder appears to have considered the building of a new kind of shell (spat shell) around the edges of the larval shell as the mark of distinction between a larva and a spat, and that consequently when a larva first settles down and becomes attached it remains a larva until the spat shell can be detected. In this sense Fig. 3 would represent a larva, and if the animal represented by Fig. 1 were to live and grow until it reached the size of Fig. 3, it would throughout this time continue to be a larva. But this is contrary to all zoological understanding of what constitutes a larva; an immature but free-roving and independent stage in the life-cycle of some animal and having different habits and a different form from the adult. The difference may be, and generally is, so great that the larva and the adult would upon first acquaintance be regarded as different species or even as belonging to different classes of the animal kingdom (e. g. a caterpillar and a butterfly or a tadpole and a frog). The transformation (metamorphosis) of the younger into the older state is not a sudden process, but the change of habit may be and will then form the best mark of division between the two stages. When an old, full-grown, free-swimming or free-creeping, umbo-shelled larva of an oyster first settles down and attaches itself to some object, as a rock or shell, it becomes a young spat, although its organization remains for a time more like that of the larva than like that of a grown oyster.

Winslow has been referred to (p. 30).

Rice (1883, p. 28): "Thus equipped I began work early in July and was able before I left the city to present to the gaze of those interested in this class of bivalve, young oysters which had been kept alive for 14 days, and were at that time apparently strong and healthy. About 44 hours after the ova had been impregnated, one of the young oysters, which had developed so far as to be entirely enclosed by its two shells within the field of the microscope, thrust out a portion of the velum and firmly secured itself to the glass slide upon which it had been placed."

Rice divided the life of the developing oyster into three portions: (1) a free-swimming condition; (2) when covered by a shell, unattached, not capable of moving freely from point to point, except to whirl about, and thus to roll around upon whatever substance it may rest; (3) attached, including the proboscis stage.

Jackson, referred to (p. 30).

Nelson, referred to (pp. 21, 24, 28, 31).

In the preceding quotations it has been shown how oyster larvæ have been obtained from the gill-chamber of the European oyster, and how raised from eggs of the American oyster. It may be pointed out here that the third method of obtaining them conveniently and in vast numbers is by means of the plankton net as first practised in Canada and by myself. The idea had occurred to others but had not been put into practice. My own employment of the plankton net for this purpose was not due to any knowledge of these suggestions for I did not know about them until several years after I began the practice. At St. Andrews, five years before, and at Canso, three years before, I had used nets to collect other plankton organisms.

Huxley (1883, p. 53): "It is obviously useless to speculate upon the causes of a 'failure of spat,' until, by the examination of samples of oysters from time to time, and by sweeping the superjacent water with a fine towing net, the exact nature of the particular case of failure has been ascertained."

Horst (1884, p. 905): "I have been disappointed in my attempts to procure oysters in these phases of development by means of catching larvæ floating about in the sea. Although I have several times fished in the neighbourhood of places containing collectors, by means of a trawl net, I only once succeeded in capturing some oyster larvæ, although they doubtless move about in the sea for several days."

Brooks (1880, p. 57) speaks of his "failure to find any floating embryos in the open ocean.......... After the middle of July I found a few embryos at the surface of the water of the Sound."

Prince (1895, p. 13): "In my investigations upon the Pacific coast, in the Dominion cruiser 'Quadra,' I captured many small embryo oysters several miles from any known oyster areas." These, if they were oyster larvæ at all, must have been of the British Columbia oyster, but it is not stated how taken or how recognized to belong to the oyster, and there is no evidence in the paper to prove that they were not larvæ of some of the other numerous bivalves of the British Columbia coast, for at that time

bivalve larvæ had not been distinguished, and it was only possible to guess at which was which."

Nelson (1903, p. 435) "discovered many swimming, shelled embryos in the high-tide water. These were secured by filtration through Schleicher and Schüll filter paper."

Nelson (1906, p. 316): "In order to ascertain whether or not oyster fry are present in the water it is necessary to filter it through a fine filter, which is a slow process."

McBride (1904, p. 151, 153): "But judging from the size of the free-swimming larvæ caught by the tow-net.................. During the latter part of the month (August) the waters were swarming with larvæ, which from their exact agreement in shape and appearance with the larvæ of the European oyster, were doubtless the later stages of the free-swimming young of the Malpeque oyster.............. The later larvæ which were captured by the tow-net are characterized by possessing a straight-hinge to the shell totally unlike the hinge of the adult..........Fig. 4. 'Late larva of the oyster captured by the surface-net.'"

These statements might have passed if the author had not inserted a figure. This shows at once that the larva was not a late larva, at least in the sense of being old, which, when taken in connection with the words "later stages", must have been the one intended. In the sense of being late in the season the statement does not correspond with what I found at the same place in the succeeding year. Upon examining "Fig. 4" closely I found that it was not an oyster larva at all. The measurements are 83, 70, 51 mm., which, if divided through by a common divisor such as will reduce the length to that size of my series corresponding in shape and structure, will give 15, 12·6, 9·2 as the length, height and hinge-line. Referring this to the table of comparison of a mussel, a clam and an oyster at this period (p. 36), it becomes evident that it could have been no other than the larva of the common clam. This conclusion is also borne out by its small size so late in the season (clams continuing to breed late), its shape, the one end being larger than the other, the relatively long hinge-line, and the chances that it would be one of the commonest of larvæ in the water about the station. Clams live in the mud along the beach below where the station stood.

Neither can "Fig. 3" be the larva of an oyster, because of the single otolith figured in each otocyst, which is true for the clam but not for the oyster. Single otoliths are present in clams, quohaugs and scallops; numerous otoconia in mussels, silver-shells and oysters; which of course could not be known without an extensive study of these bivalve larvæ. The expression "Otocysts..........here recorded so far as I am aware for the first time" is very similar to the statement of Lacaze-Duthiers (1854, p. 1200). "Enfin j'ai vu apparaître les otolithes..........quelques globules agités de mouvements..........dont personne n'avait même constaté l'existence." The words "quelques globules" show that Lacaze-Duthiers had observed the character of the otoconia.

Notwithstanding the mistaken identity of species the author thought he saw an "exact agreement in shape and appearance with the larvæ of the European oyster."

It is announced that, "It was my special object at Malpeque to determine the time at which the oyster became sexually mature, as it is the object of the Government so to frame its regulations as to protect the oyster during this period of its existence...... When I commenced to take observations at the end of July, etc." The author made the mistake of commencing a month to six weeks too late to accomplish the proposed object, which occasioned still other mistakes besides those referred to.

VI

ORGANS OF THE LARVA

Shell.—The shell in growing (Plate I, figs. 10-21) scarcely increases the length of the hinge-line, but it soon shows a tendency to become slightly pointed in front, and to exhibit delicate, concentric, semi-circular lines of growth, apparently under the centre of the hinge, but in reality somewhat laterally from it. With further growth this part of each valve becomes raised into a prominence, the beak or umbo (Plate V, fig. 31, *um*), which projects upwards, backwards and outwards, and gives to the later stages of the larval shell a different appearance from the earlier ones. The difference becomes distinct at about 25 units length (Plate I, fig. 15), so that this size may be regarded as dividing younger straight-hinge larvæ from older umbo-stages. The shell of the largest free-swimming larva I have a record of, measured 56 x 52 (56 x 6.9 μ= .386 mm.). Whole numbers of small units are more easily grasped than fractional parts of large units; so I have used measurements of the shell from 10 to 56 (micrometer units), rather than from .069 to .386 mm. From 69 to 386 μ (micro-millimetres) could also be used.

The straight-hinge stages are thin from side to side and the valves are symmetrical or nearly so; but the umbo-stages become thick from umbo to umbo, although thin anteriorly and below, and the left valve is larger and more convex than the right. On this account specimens mounted on a slide appear of different shape, depending on the size and on the side upon which they are lying, for when one valve is pressed flat against the slide the hinge-line will be tipped towards the observer so much, it may be, as to expose the dorsal portion of the under valve. On account of the greater size and convexity of the left valve, and especially of its large umbo, the tipping is greater when this valve is below and both umbos (umbones) are largely exposed. When, however, the larva is lying on its right side the small right valve is more completely covered by the larger left. Because of the different positions possible from various degrees of tipping or rolling, the measurement of length is safer for comparison than that of depth (height). The following are some measurements giving length, depth and length of hinge-line:—

*10 x 8 : 7	(10 x 9 : 7)
11 x 9 : 7	(11 x 10 : 7)
12 x 10 : 7	(12 x 10.5 : 7, 12 x 10 : 7.5, 12 x 10 : 8)
13 x 11 : 7	(13 x 11 : 7.5, 13 x 11 : 8)
14 x 12 : 7	(14 x 12 : 7.5, 14 x 12 : 8)
15 x 13 : 7	(15 x 14 : 7, 15 x 13 : 6.5, 15 x 13 : 7.5, 15 x 12 : 8)
16 x 14 : 7	(16 x 14 : 8)
17 x 14 : 8	(17 x 15 : 7, 17 x 15 : 8)
18 x 15 : 8	(18 x 16 : 7)
19 x 16 : 7	(19 x 18)
20 x 16 : 8	(20 x 18, 20 x 20)
21 x 17 : 8	
22 x 18 : 8	(22 x 21)
23 x 19 : 8	
24 x 21 : 8	
25 x 21.5 : 8	
26 x 22 : 8	
30 x 28	
35 x 32	
40 x 38	
45 x 42	
50 x 43	
55 x 50	

It will be seen that for the same length there are small variations in depth and in the length of the hinge-line. Most of these are not true variations, but due to slight differences in position, which are more common in proportion to the growth of the umbos. I have not given measurements for all of the even numbers above 25, because from this size up there is no excuse for mistaking the oyster larva for that of any other bivalve.

The colour of the straight-hinge shells is light gray, but the older umbo-stages become darker horn-coloured. A few irregular teeth may be seen along the hinge-line, which is as a rule rather straight, but may be slightly hollowed, or have anterior and posterior hollows, being higher in the middle and at each end. With the growth of the umbos the characters of the hinge become obscured, from the fact of its having to be seen through one of the valves, or else from above, which changes the direction of observation.

The colour of the living larvæ changes in passing from the younger to the older stages. The youngest are uniformly grayish, but even at a length of twelve there may be a faint tinge of pink, and at 14 a shade of yellow in the position of the liver, which at 17 has deepened to brownish.

**Explanation*: 10 x 8 : 7, i. e. length 10, depth 8, length of hinge 7 (measured in micrometer units).

At 20 the general shade is distinctly reddish brown, which becomes deeper with advancing growth. This tint is characteristic of the oyster larva, and of itself can serve to distinguish the older stages from every other bivalve larva. At first I supposed it had to do with the red sandstone rocks, that in Prince Edward Island form such pleasing contrast with the green herbage above them, and influence the apparent shade of the water and its reflections, the mirage, the beach, the great sand-dunes, the roads and even the people, who are sometimes nicknamed "Redfeet." But the oyster larvæ of Caraquet and other places along the New Brunswick coast present the same reddish-brown colour, although red sand-stone rocks are absent and larvæ of mussels, clams, quahaugs and the rest are not red, even at Malpeque.

In the larger larvæ the colour becomes so deep as to interfere with the transparency, but wherever soft parts, as the mantle, are protruded beyond the edge of the shell they are of a distinct pink.

Velum.—When mounted on a slide and covered with a cover-slip, living larvæ are generally quiet, with all parts withdrawn into the closed shell. If the cover-slip is supported so as to accommodate a greater depth of water, however, a few of them will soon show signs of life. To encourage this, fresh sea-water of the same temperature as they are accustomed to should be used, and for low powers of the microscope an open watch-glass may be conveniently employed, instead of the slide and cover-slip.

Of the parts that can be protruded beyond the bounds of the shell, the most conspicuous is the velum. At first the larva is covered with small cilia, except in the region of the shell-gland. The broader anterior end develops a crown of longer, thicker, more powerful cilia, the ciliated disk or prototroch (Plate I, figs. 9, 10, 11), which in the trochophore, as well as in the youngest shell-bearing stages of the veliger, is a stiff, fixed organ, incapable of lateral movements, folding or retraction. But, parallel with the growth of the shell, there are muscle-fibres differentiated, which can now find a solid place of insertion. Some of these extend from the prototroch to the region of the umbos and soon become effective in withdrawing the swimming organ back between the shell-valves. The changes in growth of the shell, which result in broadening its posterior end and in carrying the umbos backwards, are no doubt correlated with the requirements for room to retract the prototroch and to give a distant insertion to the retractor fibres. As the viscera become crowded backwards the prototroch grows larger, and acquires a degree of freedom from the rest of the body by a constriction between the two. This permits free expansion of the margins and increases the surface and swimming power of the organ of locomotion, which can arch over the anterior end of the shell somewhat like a veil, hence the name 'velum' (Plate I, figs. 12, 13, 14, 15, 19, 20). In being withdrawn into the shell it folds up the middle (Plate V, fig. 30),

corresponding with the slit between the valves, its two halves turning forwards and then crumpling into smaller, secondary folds. The surface of the velum is ciliated, its front margin carrying rows of especially large, powerful cilia, which are the chief propelling agents. Their movement can not ordinarily be observed in active life, exhibiting only a shimmering of the surface, but sometimes in enfeebled, injured, or dying individuals the strokes of the cilia are so slow that it is an easy matter to see how the locomotory effect must depend upon a simultaneous, vigorous, bending stroke in one direction, followed by a slow return to the original position. The velum precedes in locomotion, dragging the heavy shell and contained body suspended beneath and behind it. In viewing the movement under a low power, it is very difficult to follow the movements of a swimming larva. It generally circles round and round or in a spiral, but sometimes goes straight ahead until it bumps into something resistant, when it jerks in its velum and snaps its shell-valves together, dropping to the bottom. In a watch-glass one can sometimes find a larva floating, with its velum expanded on the surface of the water and shell suspended below (Plate V, fig. 29), or creeping, with its velum pressed flat against the glass and shell carried above (Plate V, fig. 28). In such positions the shape of the velum is elliptical or oblong-elliptical, thin at the margins, but thick towards the centre, where it is attached by a broad stalk to the body.

The velum has been known since Leeuwenhoek (1695).

Foot.—A second organ of locomotion, capable of protrusion from the open shell, is the foot—an organ unknown for the oyster until 1904, when it was discovered by myself. In adult bivalves generally the foot is such a characteristic organ as to have suggested one name (Pelecypoda) for the class, notwithstanding the fact that there are a few genera in which it is absent or greatly reduced. Of these the oyster and the silver-shell are the commonest. Spat and adult oysters are normally fixed to rocks or shells, to which their left valves are solidly cemented. Under these circumstances a creeping foot, such as is possessed by a clam, a quahaug, or a mussel, would be of little or no service to an adult oyster, which as a consequence has failed to retain it. Its absence from all sizes of oysters down to microscopic spat stages is doubtless chiefly responsible for the hitherto universal belief that the oyster does not possess a foot at any stage of its life. If the grown stages differ so widely in habit and structure from the polecypod type, why should not the larva also? The young stages of the larva known to and figured by various investigators do not possess a foot.

Influenced by such facts of morphology, physiology, and embryology, zoologists could not resist the conclusion that the oyster larva is very different from other common bivalve larvæ, that were known to possess a foot, in that this organ is absent in the oyster larva, which must promptly

settle down at an early age to a fixed mode of existence like its parents. The fact that both of these conceptions have been proved wrong by my study of plankton stages justifies the correctness of the view with which I started out, viz., that plankton stages had been neglected, embryologists having jumped from early veliger to young spat periods.

On the other hand there appears to have been a predisposition to expect some vestige of this organ which will account, perhaps, for a few references to it in the literature, although the early stages to which these references are applied possess no organ that can justly be regarded as such.

The first appearance of the foot in development is difficult of recognition on account of close union with the abdomen, of which it is a ventral outgrowth. It is further obscured by the overlying shell, mantle, gills, and by the lack of colour and of movement at this period. It is not until the larva passes into the umbo stages that the foot becomes recognizable from its movements. By the time the shell measures 35 and over, the foot is becoming a well developed, active, and most capable organ. It is formed as a muscular creeping surface along the ventral edge of the abdomen, behind the velum and mouth, and grows forwards and downwards until its distal end acquires an amount of freedom sufficient to perform feeling movements over all parts of the body of the larva, both inside and outside of the shell. (Plate I, figs. 19, 20; Plate V, figs. 30-32; Plate VI, figs. 2, 4). These movements are quick, nervous and wormlike, always ready to instantly jerk the organ back to its position of rest within the shell, where it lies closely tucked away behind the velum and between the gills. When being protruded, it is at first short and tongue-shaped, but as it becomes further extended it assumes a narrow ribbon-like form as long as the length of the shell. In creeping locomotion, the foot is stretched forwards and flattened against some object to which it clings, and then, by contraction, the body and shell are dragged ahead and the process repeated. To facilitate adhesion the under surface is flattened and sometimes appears grooved even to such an extent as to permit the two halves to fold against each other longitudinally. It is possessed of relatively great muscular strength, as evinced by the way in which it jerks the shell about and flops it from side to side. The surface is uniformly covered with fine cilia in active motion. Near the base of attachment there is a posterior heel-like projection which, when the foot is fully extended, is likewise carried beyond the limits of the shell. The heel is the papilla upon which opens the duct of the byssus gland, situated along the axis of the proximal part of the foot (Plate VI, fig. 5). In each side of the base of the foot is an otocyst in apposition to the surface, and between these a pair of pedal ganglia.

When the animal is at rest or swimming, the foot is shortened, withdrawn and compactly folded away so close against the abdomen as hardly to be observable. It is rarely to be seen protruded at the same

time with the velum—since it is used only when the larva is lying or creeping on the bottom. In development, phylogenetically as well as ontogenetically, the foot is a later organ than the velum. The velum is capable of more free and rapid locomotion when the animal is small and light; the foot becomes of greatest service towards the end of the free-swimming period, when the animal is larger and heavier and, due to failing powers of the velum, it is obliged to sink more frequently and for longer periods to the bottom. Here it must often settle into soft ooze, mud, or sand, or be overwhelmed with sediment, in which circumstances the foot might be of life-saving value in extricating it and creeping on to a solid substratum. But, judging from the relative size of the byssus-gland and byssus-papilla, it would seem that the existence of the foot has a broader significance, in that it may be most useful in selecting a suitable place for fixation and in furnishing a byssus-secretion for the first cementing of the shell fast to some rock or other object. The length and shape of the byssus-papilla (heel) is sufficient, with the stretching powers of the basal part of the foot, to bend round the edge of the shell and bring secretion to the point of contact. In doing this the foot and byssus-gland would still be preserving their original function of clinging and fixation. It is conceivable that of the original, scattered, unicellular glands, that protected the surface against chemical action of water, some, situated along the sole of the foot, became specialized to smoothen the way in creeping, or were of advantage in the exclusion of water in clinging, and that, further, these became united along a common duct and sunk farther below the surface to form the byssus-gland.

That the foot was primarily a clinging organ is supported by such existing primitive mollusks as Chiton and Acmæa. Yoldia, Nucula and other bivalves still retain the flat-soled clinging and creeping foot. The mussel, the clam and the oyster exhibit three different methods of specialization from such a creeping condition. The mussel becomes attached by its byssus, the clam burrows, and the oyster is fixed by its shell, and as a result each becomes correspondingly modified. But the young of all of them still pass through a free-swimming and then a creeping condition, in which there is a clinging and creeping foot provided with a byssus-gland. The mussel retains its byssus organ and the reduced foot containing it, the clam loses the byssus but develops the foot to a burrowing organ, the oyster loses both, having become fixed by its shell. Discovery of a foot for the oyster brings this genus into line with what is known about other members of the group.

Lacaze-Duthiers (1854) wrote: "En avant de l'anus un appendice peu saillant simule un rudiment de pied." From the translation by Horst (1884): "Soon the shell has grown so large that it inclosed the entire body; in front of the anus there is found an appendage resembling a rudimentary foot.........The mouth seems to be placed between the trochal disk and the foot-shaped appendage in front of the anus; it is a long funnel lined with vibratile cilia, the upper lip being formed by the disc itself, and the lower lip by the appendage in question."

If we refer to Horst's (1884) Fig. 15 or 16, or to Huxley's (1883) Fig. 3 A, it will appear altogether probable that the foot-like appendage was in reality the lower lip, as in fact Lacaze-Duthiers states. There is nothing significant about the expression, "in front of the anus," since at this period mouth and anus are not far apart, and the thickened lower lip is prominent. All the references to velum (trochal disk), shell, mouth, stomach, liver-granules, intestine, muscles, otoliths, or other organs, refer to a larva in the young straight-hinge stage, when a foot is not yet developed. It must be remembered that the only method of procuring larvæ at the time was by taking them from the parent European oyster, and that rearing from eggs and capturing in plankton were unknown, as were also the older straight-hinge and all the umbo stages, and it was not suspected that larval life continues for so long a time as it does, or can be divided into clearly marked periods. A young larva is clearly referred to in the stiff, fixed type of trochal disk: "Even in the more developed larvæ neither branchia nor heart could be observed, not any movement of the trochal disk as stated by Davaine."

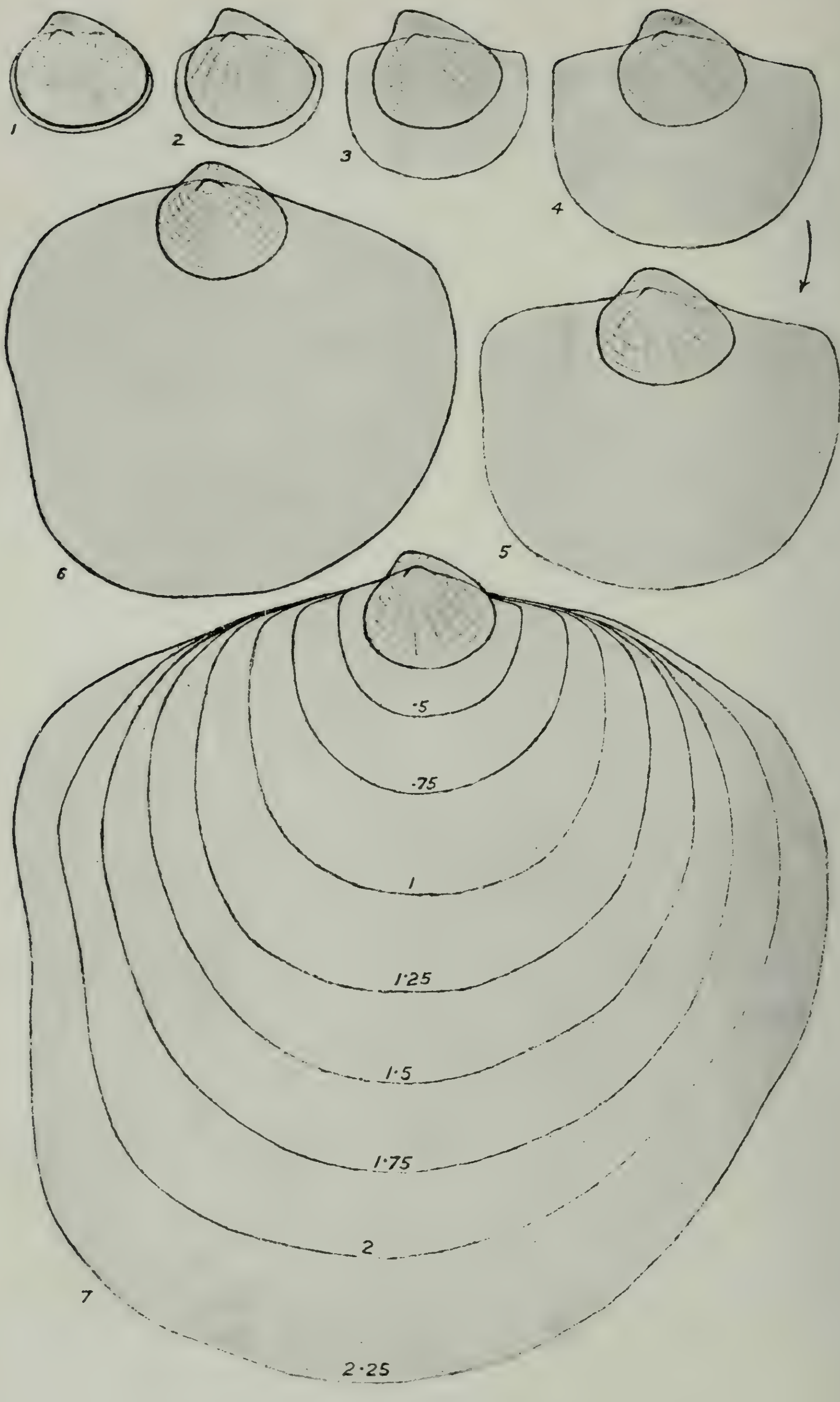
Brooks (1880) made the statement: "Near the centre of the ventral surface—the top of Figure 32—there is a well-marked and constant protuberance of the body wall, which occupies the region which, in most molluscan embryos, gives rise to the foot, and which may perhaps be regarded as a rudiment of that organ." In the same paragraph, and referring to the same figure, he mentions "the primitive digestive cavity", and on page 68 "the primitive digestive tract opens by a wide blastopore," while on page 54 referring to a slightly later phase he said: "The foot-like protuberance on the ventral surface has disappeared, and the blastopore on the dorsal surface has entirely closed." No one would claim that the part referred to in these extracts is the same organ as I have described in very much later larvæ. The protuberance could have nothing to do with the foot. It disappeared long before the true foot was developed. It was on the dorsal surface (not ventral as Brooks thought at the time). Even if we admit that it was ventral a comparison with Fig. 37 will show that it was situated in front of the mouth, which could not be possible with the foot. That Brooks changed his view may be seen in his book of 1905, Fig. VIII, where the depression behind it is regarded as the shell-gland. Moreover it would precede the shell in time and be the first molluscan character to appear.

Horst (1884) stated: "The portion on the ventral side, situated below the mouth, now begins to protrude very strongly, so as to form a sort of foot which causes the embryo to resemble a young gastropod. The blastopore continues to be very distinct." Referring to his Figs. 9, 10, we observe that it is only an accidental prominence, since it is bounded below by the invagination of the blastopore and above by that of the shell-gland, and further, it disappears later on as in his Figs. 13, 14. The so-called foot of Lacaze-Duthiers, of Brooks, and of Horst are three different parts.

Jackson (1890): "The nearest approach to a foot known in the developing oyster is that shown in Fig. 24, p. 299, and I discovered no traces of a foot in my youngest specimens.............. The fact that a velum, or swimming organ, exists up to the period of permanent fixation, accounts for the great reduction of the foot, because that organ is unnecessary while the animal is provided with another locomotive organ, and is useless for progression after the animal is permanently attached." The figure referred to is that of Horst, Fig. 15, where the reference is clearly to the lower lip, at a stage considerably later than that for which Horst claimed a "pediform appendix."

The best that can be said for all references to a foot in these early stages is that, by comparison with other species, they indicate the place where, at a later date, through growth and specialization, a foot as well as several other parts are formed between the mouth and the anus; zoologists by inference from comparative embryology were prepared to find a rudiment or a vestige of this very characteristic molluscan organ.

Mantle.—The mantle continues to grow downwards as two fleshy folds right and left of the body (Plate VI, figs. 1-9), to which they are attached along the dorsal region. The lateral flaps are thin and the margins free below, in front and behind. They lie against the inner sides of the shell-valves and are responsible for the growth of the latter. The edges form a thickened rim, containing unicellular glands, and supporting irregular processes resembling tentacles, that sometimes protrude beyond the margin of the shell.



SPAT
(Enlarged 50 times)

KEY TO PLATE II

Figs. 1–6. Oyster spats at different short intervals after fixation, for the sake of space reduced to one-third the magnification of fig. 22 of Pl. I., now magnified 50 diameters.

The larval shell (prodissoconch) maintains the same size as long as it can be recognized in a spat. Larval shells of all spats maintain approximately the same size, no matter how large the spats grow. In all the figures the prodissoconch is shaded, the dissoconch only outlined.

The spats soon become so large that a lower power objective has to be used in order to see the whole spat at once.

Fig. 1. Spat with a very thin rim of new (spat) shell.

Oc. 5, obj. 4=55 x 6·9=·379 mm.

Oc. 5, obj. 2=24 x 15·38=·369 mm.

·369 x 50=18·5 mm.=approximately the length of the larval shell as it appears in the figures.

Fig. 2. Spat ·4 mm. long.

Fig. 3. Spat ·5 mm. long.

Fig. 4. Spat ·75 mm. long.

Fig. 5. Spat 1 mm. long.

Fig. 6. Spat 1·25 mm. long.

Fig. 7. Eight spats superposed so that the larval shells coincide—the same effect as a single spat drawn at different stages in its growth from ·5 to 2·25 mm.

[illegible]

[illegible]

[illegible]

[illegible]

Gills originate in this period of development. They begin as a ridge along each side of the body, underneath the mantle and above the base of attachment of the foot (Plate V, figs. 30-32; Plate VI, figs. 4, 5). Each ridge soon becomes segmented by external transverse creases into a series of short papilla-like processes, diminishing in size from before backwards—the last ones being mere knobs. In the oldest free-swimming larva there are about eight filaments in a series, the left being best developed; their lower ends free, but their upper ends joined in the axis that extends backwards and is united with its mate of the opposite side porteriorly behind the foot. They are at first solid but later become hollowed from above. These two series continue to develop into the right and left inner series of filaments of the adult oyster.

Adductor Muscles extend transversely between the valves of the shell (Plate V, figs. 30-32; Plate VI, figs. 1, 6), an anterior, at first larger, one in front of and above the velum, and a posterior one below the hinder parts of the umbos, which becomes the single great permanent adductor of the adult oyster. The anterior adductor was known to Huxley (1883), who argued that it could not be the permanent adductor. The posterior adductor was discovered by Jackson (1888). Retractor muscles converge from the umbos to the velum and to the foot and there are intrinsic muscle-fibres in the velum, the foot and the mantle.

The Intestinal Canal.—(Plate V, fig. 31) increases until it is much longer than the body and in consequence has to become folded, the greater part lying left of the median sagittal plane, but mouth, œsophagus and anus are median. The mouth is a funnel-shaped opening lying immediately below and behind the velum, to which its walls are attached and with which it is protruded and withdrawn; so that it can only be functional when the shell is gaping and best when the velum is to some extent expanded, the activity of its cilia perhaps contributing to the process of feeding. In sections, cilia of the inside of the folded velum point inwards to the mouth. The œsophagus lies between velum and foot in the median sagittal plane as well as in or very near to the median transverse plane of the body. Here it passes towards the dorsal region, between the first gill filaments of opposite sides and opens into the stomach which is provided with large, brown, lateral liver-sacs. The intestine passes backwards towards the right and then forwards towards the left, when it again turns backwards and upwards in the left umbo and finally, as rectum, downwards in the median plane, over the heart and posterior adductor muscle to the anus.

Pigment Spots (eye-specks) appear in larvæ of about 40 units length —one on each side—as conspicuous black spots, Viewed from the side (Plate V, figs. 30, 32) they appear to be about the centre of the animal, anterior to the gills. In sections (Plate VI, figs. 3, 5) they are found to

be right and left on the lateral walls of the body, just in front of where the ectoderm becomes continuous on to the outer surface of the base of the first gill-filaments.

Otocysts (ear-sacs) occur right and left, below and behind the pigment spots as viewed from the side of the larva (Plate V, fig. 32; Plate VI, fig. 4). In sections, where their position can be determined more accurately, they are found to be placed laterally in the proximal part of the foot, close to where its ectoderm passes over on to the inner surface of the first gill-filaments. Each cyst contains about a dozen small otoconia (ear-motes).

Nerve Ganglia are to be found in three pairs. The first or supra-œsophageal, cephalic ganglia (Plate VI, figs. 3, 9) form a mass (neural plate) at the centre of the base of the velum, in front of where the œsophagus joins the stomach. They are protected in front by what appears in longitudinal sections to be a yellowish-brown, flexible, chitinous layer, from which arise muscle-fibres of the velum. Behind the œsophagus and between the otocysts are the pedal ganglia (Plate VI, fig. 4), connected by a commissural nerve. Large visceral ganglia (Plate VI, figs. 6, 7), connected by commissure, are placed apart, in front of the posterior adductor muscle.

The Heart (Plate VI, figs. 6, 9) or a vessel containing what appears to be blood cells, is situated above and in front of the posterior adductor muscle and more towards the right (in the right umbo) than the left side —the stomach being most to the left. Two vessels lead towards it from the sides of the base of the foot and abdomen.

Sections of Larvæ—transverse, sagittal, horizontal sections, prepared by decalcifying in weak acid to remove the hardness of the shell, embedded in paraffin to facilitate holding and cutting, sectioning with a sliding microtome, staining to differentiate and render more apparent, and mounting in the usual way in Canada balsam on a slide and under a cover-slip—have contributed towards a more accurate understanding of the relative positions, sizes, shapes and structure of the organs. Without these it is scarcely possible to study with any degree of satisfaction such parts as the retractor fibres of the velum, the vacuolated cells of the liver, the three sets of ganglia, the heart and the byssus-gland. In the older and larger living larvæ these are obscured by depth, pressure, overlying parts and pigmentation.

Sagittal sections show especially the large space occupied by the velum in front, the position of the œsophagus and foot below, the stomach and heart above, and the anterior and posterior adductor muscles.

Transverse sections exhibit the asymmetry of the shell, gills, etc., and the mantle with its thickened edges. Anterior ones show the adductor muscle, the velum, the mouth and the tip of the foot. Median ones

show the pigment spots, gills, œsophagus, cerebral and pedal ganglia with their commissures and otocysts. Posterior ones show the stomach and liver, heart, posterior adductor muscle, and the visceral ganglia.

VII

POST-LARVAL, FIXED OR SPAT STAGES

Difficulty of Discovery when Very Young.—The pre-larval or embryonic stages are free but incapable of locomotion, the larval stages free and locomotory, while the post-larval or spat stages are offset from any of the preceding by being normally attached or fixed to shells, rocks or other solid submarine objects. From this time onwards there is no further change in the method of living, the spats growing up regularly into adult oysters (Plates II and III).

Oyster consumers, merchants, fishermen, culturists, are all aware that it is possible to begin with the largest oyster and pick out a series descending in size to those of very small dimensions. Such terms as "large," "medium," "small," may have very different meanings, according to the judgments of the people using them; but sooner or later the youngest oysters of the series become so small, irregular and variable, as to be with difficulty distinguished from several other species with which they occur. We may, I suppose, regard this size as approximately that of a man's thumb-nail. Oysters smaller than this require greater care, more knowledge of other animals, and more special technical application than most people possess. I have known men who were brought up in oyster districts and used to fishing or handling oysters all their lives who had never sought out young stages; men interested in oyster questions have shown me objects (stones, shells, bark, &c.) with supposed oyster spat attached that were not oyster-spat at all; a culturist, who had been very successful for upwards of twenty years in the management of large spat, had never learned to recognize the minute young spat; a professed zoologist, working on the subject, and presumably acquainted with many types of animals and the methods of studying them, mistook for spat scale-insects on brush that had been put out for their capture. There are statements of observations that may have been made in good faith that, because of too narrow an acquaintance with the subject, refer to wrong animals. The careful investigator cannot trust anything but what is accompanied with sufficient detail to prove that the observer had a first-hand knowledge of his subject and that he had the proper objects before him. The greatest lack in the literature is detail. Off-hand, empirical statements are misleading, since they do not bear the evidence of being either theoretical or practical. It would have sometimes saved succeeding investigators end-

less trouble and loss of time if a few extra details had been inserted, especially as to measurements and drawings.

The nearest relative of the oyster that is often mistaken for a young spat-oyster is Anomia (silver-shell), which ranges in size from that of a silver ten-cent piece downwards. By one who has studied Anomias, they can nearly always be recognized at sight and distinguished from the oyster on account of their shape and surface. In cases of doubt it requires but to pry them free from their support with a knife-blade and observe the looser mode of attachment and the perforation in the under (right) valve of the shell, through which passes a short, flexible stalk of attachment. The oyster spat is fastened by cementing the whole or a large part of the left valve solidly to the supporting rock or shell.

Young, light-coloured Crepidulas are often difficult to distinguish, but they may be slid along on their attachment or pried off, when it will be observed that there is only a single shell, and in place of the lower valve or a stalk there is a broad, fleshy, clinging and creeping foot.

Colonies of Bryozoa (polyzoa) may resemble in size, colour, and shell-like surface the young oyster, but are easily distinguished by observing through a lens the assemblage of similar, distinct chambers (zoœcia).

Incrusting colonies of plants, such as Ralfsia, are misleading to those unaccustomed to the use of a lens or a microscope.

These and such-like other animals and plants, as well as the aggregation of mud, silt, ooze and other matters, make it increasingly difficult to discover the very youngest stages of the oyster-spat, which have in fact been seldom found and by a very few specialists in the subject.

At the time when I began my work on the oyster the microscopic spat had never been studied in Canada, and there was nobody here to give any first-hand information. One summer had been spent at Malpeque without any progress towards discovering it. It was apparently a very difficult subject. I at once began making observations with a view to retracing from older to younger specimens, in order to learn where were the likeliest places to find them, upon what objects they would be fixed, and what they would look like. At the same time I began experiments with a view to catching the earliest stages precipitated from the water, where presumably there were free-swimming larvæ present. Besides I rummaged through what literature was accessible to find what others had done, and to obtain suggestions.

Of the common bivalve mollusks the adults of Ostrea, Anomia and Mytilus, are fixed to objects of support. Mya, Venus, Mactra, Saxicava, Clidiophora, Macoma, Ensis, Pecten, Yoldia, Mesodesma, Kellia, Tottenia, and the rest, are free-living—creeping or burrowing—species, and, as such, might be eliminated from consideration. Mytilus could be easily recognized from its blue colour, shape, and byssus attachment. Any young fixed-bivalve was very likely to be either an oyster or a silver-shell. But,

while there were plenty of small silver-shells and Crepidulas, there were very few really small oysters, and they rarely smaller than a thumb-nail. I examined rocks, stones, shells, the lower logs of wharves, rock-weed, eel-grass, gravel, sand, and in fact everything I could think of that might possibly give results, but always without avail. As had been tried during the previous summer, I also used bundles of brush-wood; these were weighted down with stones, or tied and left floating, and were examined with a lens at intervals of a few days. All such attempts were kept up for some time, seemingly without one ray of light, only ever thickening mystery. The long distances traversed to and from the most favourable spots, the faunistic work along shores, by dredging, and with the plankton net, examination of all material collected, perusal of literature, &c., absorbed time, and it looked as if that season would pass with as little result as the preceding. Could it be that our northern oyster was a different species, with some variation in its habits from the southern one?

Use of Glass Strips as Cultch.—About this time a copy of Jackson's work (Phylogeny of the Pelecypoda, 1890) recalled a method of using glass to catch free-swimming larvæ of many adult fixed forms of animals —a method first employed by Möbius. I had become acquainted with this method some years before while working on the clam at St. Andrews, but had forgotten about it until a reference brought it to mind. This was the time to try it. Möbius had used microscopic slides. I judged that for my purpose larger pieces would be of advantage in that they would be more easily handled, not so likely to get lost, and would offer a greater surface. I had window glass cut into strips 2 x 6 inches and stood on end in crocks—each crock accommodating about a dozen pieces, that were kept from falling together by a coarse mesh-work of wire. These batteries were then planted at various places on or in proximity to oyster-beds—especially just below low-water mark off Curtain island and off Ram Island point. The crocks were partly sunk in the gravel or sand of the bottom and made secure against the buoyant force of the water at high tide and the lateral action of currents, waves, and winds at low tide, by building little pens of stones around them but leaving the tops well open. It was thought that larvæ, either swimming about or swept about by the water, might drop into the crocks, where the water would be comparatively still, and find it easy to cling to the glass during the first stages of fixation.

Ram Island point is a most favourable place, since it has a rocky, stony, gravelly or sandy bottom, with an adundance of small-sized oysters so thickly set that in places it is impossible to step without treading on them. The tidal current coming from the upper bay (towards Summerside) passes along both sides of Curtain island and, joining with that from Malpeque on the one side and from Grand river and Bideford on the other, sweeps over or past this submerged point on its way to the narrow mouth of Richmond bay, carrying water (and presumably larvæ) from almost all

parts of the bay. This is about six miles from the station but daily visits were made, the strips of glass were one by one withdrawn and examined with a lens, and, whenever a suspicious looking speck was observed, the glass was put into a pail of sea-water and taken to the station to be examined with a compound microscope.

The glass strips were not too big to be used on the stage of a microscope, either side could be equally well examined, either reflected or transmitted light used. In the crocks they soon become dirty, receiving a slimy coat speckled with sediment, plants and animals. Standing the strips vertically in the crocks minimizes the amount of sediment that clings to them, and a smart sweep through the water, when removing them, washes away a good deal of that deposited, without carrying away spat, which are too firmly fixed. The method has a broad application. There are bacteria, diatoms, algæ, protozoa, sponges, hydroids, polyzoa, worms, crustaceans, snails, bivalves, and other forms caught, either attached, clinging to or creeping over the surface. It seemed as if everything but oysters could be obtained. This went on for some time. So far as I could see I had neglected nothing. Could it be that there were no oyster larvæ in the water? My work on bivalve larvæ, which I had been pursuing side by side with these experiments, had already singled out a particular larva of a different appearance from all the rest, that had been increasing in abundance, but whether it was an oyster or not depended upon whether it could be caught on the glass and recognized as an oyster-spat.

At length, on the 16th of August, I discovered a single minute oyster-spat, bearing unmistakable marks of recognition, and displaying both the now familiar larval shell (prodissoconch) of the plankton and the surrounding lately deposited thin rim of spat shell (dissoconch). On the 19th I found a second, and on the 22nd a third. Everything speedily became clear. My experiments had been running ahead of nature, a circumstance which, of course, I could not have known before hand. Oyster larvæ had been in the water, but they were not ready to become fixed and transformed into spat. They had to bide their time. This, as will be readilv admitted, is a very important point to the oyster culturist, for there is no use expecting results until the proper time arrives. I had caught a few of the very first spat of the season. The small ones obtained earlier in the summer were belated specimens of the previous year, which explains their scarcity and the fact that I could not find smaller ones.

Attachment to Natural Marine Objects.—After reaching this conclusion I again turned to the examination of natural marine objects, and on the 2nd of September found a spat on the surface of a half grown oyster shell. From this time onwards they were found in increasing numbers and on various objects—shells of the oyster, mussel, clam, quahaug, bar-clam, razor-clam, round whelk and stones, but they must occur on many other objects as well. Judging from the numbers of half-

grown oysters that carry periwinkle shells at their umbos, it would seem that these latter are a common base of fixation, but the dark colour of the winkle and the colonies of *Ralfsia verrucosa* it frequently bears render it difficult to find very young spat on its surface. On the other shells, after being shown specimens, the men on the steamer "Ostrea" could also find quite young spat.

Dimensions of Newly Fixed Spat. — The spat caught on glass varied of course in size—the first measured .87 x 1.03 mm. in height and length, the second 1.58 x 1.20, the third .51 x .55, the fourth .86 x .95. Similarly the first found on an oyster shell measured 2.4 x 2.3, while those subsequently procured varied from less than 1 mm. to 6 mm. in height. Of these latter a very large number was collected, so that I could easily arrange series passing by small gradations in size towards the larger spat of the fishermen. But of the smallest (just attached) spat I had few specimens.

Five years later, however, in 1909, I again had the opportunity of pursuing the subject, and I procured an abundance of the very youngest spat—many of them in fact slightly smaller than some of the largest free-swimming larvæ caught in the plankton net, which shows either that there is a certain individuality or that there is some ability to accommodate themselves to circumstances.

The largest larva I have a record of, measured 56 units (= .386 mm.) in length. The smallest spat I have found measured 53 units (= .365 mm.) in length, and I can state that it was normal in both fixation and structure, since I have a complete series of transverse sections of it. It would take nearly 70 of these placed end to end to reach over a length of 1 inch, and 5000 side by side to cover a surface of 1 square inch. There was a visible narrow rim of spat-shell added to the edge of the larval shell, and the fixation could have been at most only a few hours old.

A common size for the fixation of the larva is 55 units (= .379 mm.), as shown by the number of spats of this size obtained, as well as by the measurements of the prodissoconchs in the umbonal regions of small spats. Some of this size had no visible addition of spat shell.

Sizes of young spats I have recorded are 53, 55, 58, 60, 62, 65, 67, 68, 70, 72, 76, 80, 82, 83, and upwards, but I have many specimens which, if selected out and measured, would very likely fill in the intermediate stages.

References to the Spat.—*Sprat* (1669, p. 307): "In the month of May the Oysters cast their spawn (which the Dredgers call their spat); it is like to a drop of Candle, and about the bigness of a half-penny. The spat cleaves to stones, old Oyster-shells, pieces of Wood, and such like things, at the bottom of the sea, which they call 'Cultch.' 'Tis probably conjectured, that the spat in 24 hours begins to have a shell .... The Oysters when the tide comes in, lie with hollow shell downwards, and when it goes out they turn on the other side; they remove not from their place unless in cold weather, to cover themselves in the Ouse. The reason of the scarcity of Oysters, and consequently of their dearness, is because they are of late years bought up by the Dutch.......... The Oysters are sick after they have spat; but in June and July they begin to mend, and in August they are perfectly well. The

SPAT
(Natural Size)

Drawn by F. W. Parker

KEY TO PLATE III

Oysters from 1 to 60 mm. ($\frac{1}{25}$ to 2 $\frac{2}{5}$ inches) in length, natural size, in the same position throughout, from the right side.

First line from left to right: 1, 1·5, 2, 2·5, 3, 3·5, 4, 4·5, 5 mm.

Second line: 6, 7, 8, 9, 10, 11, 12 mm.

Third line: 14, 16, 18, 20, 22 mm.

Fourth line: 25, 30, 35, 40 mm.

Fifth line: 50, 60 mm.

(Drawn by Mr. F. W. Parker, of Halifax, N.S., medical student at McGill University, from specimens of the author's selection and under his directions).

male Oyster is black-sick, having a black substance in the fin; the female white sick (as they term it), having a milky substance in the fin." (Report U.S. Fish Com. 1892, p. 307).

Huxley (1883, p. 53): "But sooner or later, they settle down, fix themselves by one side to any solid body, and rapidly take on the characters of minute oysters, which have the appearance of flattened disks, 1/20 of an inch, more or less, in diameter; they are therefore perfectly visible, as white dots, on the surface of the substance to which they adhere. In this condition, the name of 'spat' is also applied to them.

"It is unfortunate that the same word 'spat' should be applied to things so different in their nature, as the eggs and unhatched young of the oyster, contained within the mantle cavity, on the one hand, and the young fixed oysters, on the other; while there is no familiar name for the very important stage of development which lies between these two. 'Brood,' 'fry,' and 'spat' would be very convenient names for the three stages, if 'brood' were not already in use for the smallest of the young fixed oysters. Perhaps the most convenient course will be to use 'fry' for the eggs or embryos which are contained within the mantle cavity of the parent; 'larvæ' for the locomotive stage; and 'spat' for the fixed condition."

Horst (1884, p. 910): "Fig. 19. Little oyster, about 7 days old; the height of the primary homogeneous shell is 0·24 mm., that of the secondary part, composed of prisms, is 0·15 mm." The complete height would be 0·39 mm., which is much smaller than Huxley's measurement of about 1/20 inch (= 1·25 mm.) In Horst's figure the larval shell measures ·34 mm. in length, which will give (·34 x ·15 ÷ 20 = ·25) as a real length ·25 mm. or about ⅔ that of the corresponding American shell. Taking Horst's (1882, '83, p. 386, Fig. 2) "Largest straight-hinge stage of the European oyster," of which the figure measure is 19 mm. and magnification 96, we would get its real size as 19 ÷ 96 = ·198 mm. Again taking Huxley's (1883, p. 54), statement of the size of the egg, about 1/250 inch in diameter, and Brooks' (1880, p. 13) measurement, about 1/500 inch in diameter, and we can make an approximate comparison of three stages of the European and American oysters:

	Egg	Larva (set free)	Spat (at fixation)
European..............	·1 mm.	·18 mm.	·25 mm.
American..............	·05 "	all stages free	·38 "

In which it appears that our oyster begins in an egg of only half the diameter, or one-eighth the volume, of the egg of the European oyster (Ryder 1882, '84, p. 791), but that ours develops to a larva one and a half times as large as theirs before becoming fixed as spat. The European oyster begins life with a great stock of food-yolk, is nurtured and protected by the parent while it is developing to nearly double the diameter of the egg, and only increases less than half this again during a short free-swimming period. Our oyster begins as a free egg of only half the diameter of the European, has a smaller stock of stored yolk, develops rapidly to the swimming stage, takes its own chances, begins feeding early, and continues its free and independent existence until it is one and a half times the length of the corresponding stage of the European larva.

Ryder (1882, '83, p. 387, Fig. 3) gives a figure of the youngest stage of a spat, "having just become firmly fixed." It is reversed so that it appears to show the left side. The figure measures 29 mm. and the magnification is 96 times, so that the spat itself must have been 29 ÷ 96 = ·3 mm. in length and height. I have already discussed Ryder's views of this stage.

Jackson (1890, Figs. 1, 2) gives figures showing the structure of the youngest stage of a spat caught on a glass slide. The real size of this spat would be 37 ÷ 120 = ·3 mm. It represents the beginning of Jackson's own observations, and is important as showing the anterior and posterior adductor muscles, the velum persisting although reduced, the gills, the anus, and what Jackson took for the palps, but in reality the foot somewhat shrunken and wrinkled.

Succeeding stages are shown in Ryder's Figs. 4, 5, 6, 7, (representing spat of about ·34, ·38, ·51, ·54, mm.) Jackson's Fig. 3 was about ·55 mm. high, and his Figs. 20, 21, about ·91 mm. Then come Ryder's Fig. 8, about 1·6 mm., his (1882, '84, p. 782) Fig. 2 of 3 mm., and Jackson's Fig. 4 of 5 mm.

VIII

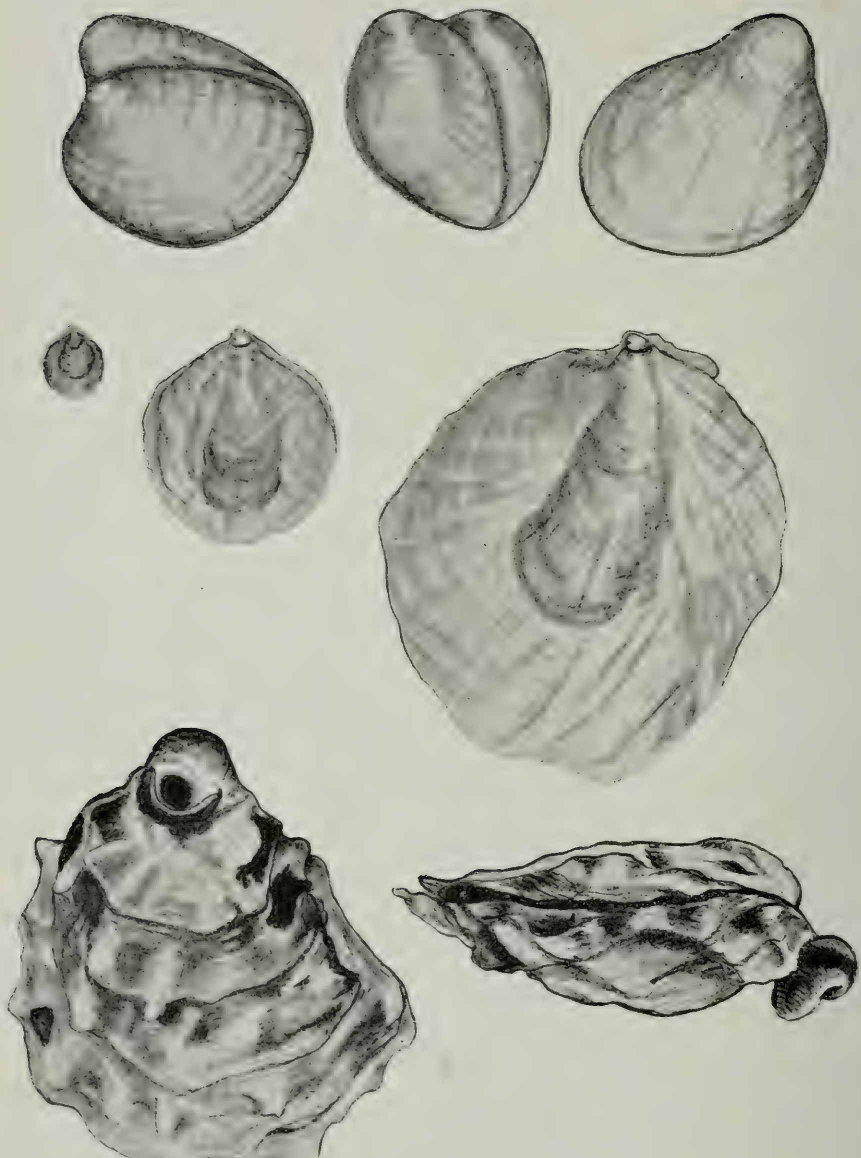
ORGANS OF THE SPAT

The Shell of the younger spats (Plate II, figs. 1-4) is longer than high, like that of the larva, and this is true not only for each valve but also for the whole shell, even when the far umbo, through tilting of the shell, stands up above the near one. At first the addition of spat shell to the anterior and posterior angles is liable to be greater than that to the rounded part below, but when about 1 mm. in height (Plate II, fig. 5; Plate III, fig. 1) the proportions become reversed, and from this time forwards the shell grows fastest below and at the postero-inferior angle. The growth is not very regular so that specimens of equal length seldom have exactly the same depths. The following are a few measurements:

55 x 55	80 x 76
60 x 59	90 x 79
70 x 67	105 x 95

The spats caught on glass exhibit the characteristic colour of the pelagic larva, the smallest varying towards pink, the larger towards brown. Jackson described his spat as "yellowish-green". Those taken on opaque objects, on the other hand, present a different appearance; instead of having a pink, reddish, or brown coloration as one would expect from comparison with the larva, or, instead of having a white appearance as might be looked for by comparison with the older spat and adult oysters, they preserve a shining, dark, metallic lustre with a few faint radial lines (Plate IV, figs. 4, 5, 6). In the centre of the dorsal region can be distinctly recognized the larval shell (prodissoconch) of the oldest free-swimming stage, presenting a uniformity of appearance in all the specimens, and measuring in the neighborhood of 55 (= .38 mm.) in length and slightly less in height.

There is another way of verifying the size of the larva at fixation: viz., to measure the prodissoconch of young spats; but it is more liable to give small variations because of the pushing of the left umbo higher upwards along the substratum than the right, the addition of spat-shell overlying the edge of the larval shell, and also because this addition causes the edges of the larval shell to be opened away from each other and the observer has to look at a different angle upon their surfaces in different cases. A few examples of measurements are:



LARVA AND SPAT

Drawn by F. W. Parker

KEY TO PLATE IV

First line· Full-grown larva of ·34 mm., from the right side, from behind, and from the left. Magnified 100 diameters.

Second line: Spats of 1, 3, 6 mm., from the right, showing the larval shell at the umbo, magnified 10 diameters.

Third line: Oyster of 60 mm., round variety, natural size, from the left side, and from the edge, attached to a periwinkle which it has outgrown.

(Drawn by Mr. F. W. Parker)

Dissoconch (spat shell)	Prodissoconch (larval shell)
58 x 50	53 x 47
58 x 58	52 x 52
63 x 62	55 x 54
82 x 75	52 x 51
83 x 70	57 x 53
90 x 79	55 x 54
105 x 95	52 x 52
110 x105	52 x 52
115 x112	54 x 54

The substance of the spat shell is doubtless deposited by the thickened rim of the mantle in layers along the ventral and terminal edges of the larval shell, but not to any conspicuous extent along the dorsal or hinge edge, where what is deposited serves more to increase the thickness of the shell and to press the umbos farther apart rather than to add to the height of the shell. This explains why the prodissoconch remains near the dorsal margin of the dissoconch during the growth of the latter, as well as explains the concentric lines of growth below the umbos. The latest deposited parts around the margins are very thin and delicate and exhibit a prismatic structure as if each prism were deposited by a cell.

At first the shape varies little from that of the prodissoconch (Plate II, figs. 1, 2), but soon the dissoconch becomes extended fore and aft of the hinge area in a manner that suggests the wings or ears (alæ) of a scallop shell (Plate II, figs. 3, 4, 5), the lower parts preserving a pretty uniformly curved outline. Later these alæ cease to be conspicuous and the whole outline may become irregular and variable. Deep or shallow concentric creases preserve more or less indication of stages of growth, and at places there may be portions of radial lines. The deeper concavity of the left valve remains noticeable for a time after fixation takes place, particularly in sections, but a little later the lower valve seems to lag behind the upper one in growth, appearing thinner and flatter, while the upper one is thicker and more curved. At a still later period the growing edge of the lower valve becomes free and the valve again acquires a deeper cavity than the upper one, preserving this difference throughout life.

While the developing oyster is free to swim or creep it is, of course, natural to describe it in terms suitable to such permanently free-living species as the clam. The more pointed end, that ordinarily precedes in locomotion and from which may protrude the velum, is the anterior end. The foot is postero-ventral to the velum. The umbos are postero-dorsal, right and left. The hinge is dorsal, i.e., between and in front of the umbos. The longest diameter is horizontal, and the height is a vertical line at right angles to the length. After fixation it becomes difficult to retain such ideals as continuously useful marks of description. At periods vary-

ing somewhat with the individual it will be found that they have become more or less modified. Viewed from the broad side and preserving the original orientation of the larval shell, the height of the spat shell soon becomes greater than the length, the hinge and umbos instead of being medio-dorsal or postero-dorsal, come to mark rather the narrow anterior end of the growing spat, and the larval shell sinks into insignificance in comparison with the spat shell. Its left valve may become obliterated by growth of the surface of attachment, but its right valve may often be found until late in the life of the spat, although it is liable to become destroyed by weathering of the umbo-region of the latter. While its position marks the anterior end of the oyster, it has long since been carried up by the umbo of the spat shell out of reach of the hinge or of the growing parts, but its anterior end still points in a general way in the direction of the anterior end of the adult. This position and relation is correlated, as will be seen later, with the increase of growth of the lower and posterior parts of the oyster's body, which occasions more or less of a rotation round the great adductor muscle, and resulting in longer or rounder forms of shells with straighter dorsal and much curved ventral border. The right, upper valve remains flatter and smoother, the left, lower or attached valve, more deeply hollowed, rougher, with more conspicuous concentric furrows or sharp over-lapping edges, and often fluted with blue-tipped projecting processes.

Asymmetry, or the greater convexity of the left valve over that of the right side, can not be due to the operation of external conditions during the present life-time of the individual (ontogenetic development). Shells that are fixed on the under sides of stones are similarly a symmetrical with those on the upper sides, although in the former case it is the right side which is turned downwards. It is inconceivable that the phenomenon is due to the mere contact of the present lifeless shell. Spats that become early separated from their attachment continue to grow asymmetrical. The asymmetry, whether of the shell or of the living soft parts, is hereditary.

Neither can the asymmetry of the present oyster have been brought about during the larval life of any or of all of the ancestors of the oyster (phylogenetic development of the larva), since both valves in that case would be developed under exactly the same conditions as in the life-time of the present larva, which is at first symmetrical.

Asymmetry must have originated during the post-larval existence (phylogenetic development of post-larval stages) of some of the later ancestors of the oyster. Since most bivalves are symmetrical, and since the young larvæ of all are symmetrical, we must believe that oysters sprang from symmetrical ancestors. Moreover, since asymmetry in its extremest forms is always associated with fixation on one side (Ostrea, Anomia), while in less marked forms it is to be found in deep-bodied species that habitually fall over on one side as soon as locomotion ceases (Pecten, Mya), we are constrained to connect asymmetry with lateral fixation or rest. It is conceivable that gravitation was the prime incentive to the occasion for fixation as well as asymmetry. That the larvæ of all of these species possess byssus-glands shows that fixation preceded asymmetry. A byssus-gland is the agent of fixation (i. e. of the conversion of a larval into a post-larval state), which is the pre-requisite for asymmetry.

We may consider that a difference in the conditions of the two sides was first occasioned when some remote but free and symmetrical ancestors of the present oyster took to a fixed mode of life, becoming attached by a sticky secretion from the foot; that the deep shell tended to fall over on one side (say the left), permitting the secretion to flow between the shell and the substratum; that the difference in the condition of the two sides gradually brought about a difference in the size and structure of the two sides; that this difference became so deeply impressed into the system as to become hereditary; and that, further, it began to precede in the life of the individual the period of fixation

which originally called it into existence (cænogenesis). There may have been an advantage in the gradual shifting of the asymmetry from post-larval to larval stages of the offspring, such as determining that the heavier side, when swimming or creeping movement ceases, should promptly come in contact with the point of fixation and at the same time insure the most favourable relative positions for the activity of organs whose functions had been perfected under like conditions in more adult stages.

The temporary transfer of the greater convexity to the upper valve in young stages of the spat can be explained by the fact that for a time the growth of the lower valve follows, as it is cemented to, the surface upon which it rests, while the upper valve is free for growth in every direction. When sufficient surface of attachment is secured the edge of the lower valve becomes free, and then the greater convexity soon reverts to the left valve again.

Two larval locomotory organs soon disappear under the new conditions brought about by fixation, viz., the velum and the foot.

The Velum, it has been thought, may become converted into some other organ (palps or gills), or it may become lost by dehiscence.

"It has been suggested by *Loven,* though without any direct evidence, that the labial tentacles of adult Lamellibranchiata are the remains of the velum. The velar area is in any case the only representative of the head." (Balfour 1880, p. 215).

"*Davaine* makes the statement that the velum appears to drop off some time about the end of the larval period. *Gerbe,* on the other hand, asserts that the velum is transformed into the palps" (Ryder 1882, '84, p. 790).

De la Blanchère thought it probable that the gills originated in the velum (Horst 1884, '86, p. 896).

Ryder says: "The detachment of the ring or crown of vibratory filaments or cilia from the embryo as asserted by Davaine has not been confirmed by any other observer" (1882, p. 404).

From the straight-hinge larva, such as was the only stage known to the above mentioned observers, to the fully formed spat or oyster, possessing palps and gills, was a long jump; yet the presence of a velum in the first and its absence in the last, coupled with the absence of palps in the first and their presence in the last, together with their anterior position and close association with gills of very similar appearance, was sufficient, in the absence of any more definite information, to suggest the connection. If De la Blanchère had been acquainted with the older umbo-stages of the larva he would have known that velum and gills exist at the same time, which would have disposed of the possibility of one being converted into the other.

The view of Lovén and of Gerbe, that the velum is destined to give rise to the labial tentacles (palps), and that therefore it does not become entirely useless and completely disappear, is a fascinating one, that seems to be supported by several bits of evidence. It is, however, not easy to picture to one's self exactly how the transformation might come about. It must be remembered that the velum is in front of the œsophagus, while the palps are behind it. Davaine seemed to think that the mouth perforated the disc of the velum, in which case matters would have been easier. The two anterior, outer or upper palps, forming a pair, are connected by a rim around in front of the mouth or open end of the œsophagus, thus constituting a sort of upper lip. In like manner the two posterior, inner or lower palps form a pair and connect by means of a lower lip behind the mouth. In the larva (Plate V, fig. 31) there is a minute free rim to the outer end of the œsophagus, often flattened out as if absent in front, the rest of the œsophagus being bound up with the median part of the posterior surface of the velum. When the velum is retracted the œsophagus occupies a somewhat vertical position, curving gently backwards and then forwards, and the mouth is full length of the œsophagus below the stomach and full depth of the velum below the anterior adductor muscle. When the velum is protruded the œsophagus comes to be stretched out in front of the stomach, and the velum is now above the œsophagus, but still separating the mouth from the anterior adductor muscle. In the spat, after the disappearance of the velum, the mouth comes to be fixed in front of the stomach, in a position just behind where the anterior adductor muscle used to be. During the metamorphosis of the larva into the spat the œsophagus would have to move broad-front up through the velum, splitting it in the median sagittal plane into right and left halves along its main vertical line of folding; each half would then have to become secondarily folded to give rise to the anterior and posterior palps of its own side; the posterior palps of opposite sides would have to grow around the œsophagus in order

to connect with each other posterior to or below it; and then all four palps would have to be turned backwards, flattened out, and have the base of attachment extended some distance along the sides of the abdomen; the surfaces of the two palps of each side turned towards each other would have to become ridged, perhaps along tertiary folds of the velum, and the cilia become increased and re-distributed along these ridges, while the other surfaces of the palps would become plane. Thus the velum would have to become relatively reduced, remodelled, changed in position, attachment, folding and ciliation. Moreover there must be a more intimate relation of the ciliated epithelium of the palps to that of the inside of the mouth and œsophagus than exists between the velum and the mouth, although when the shell is gaping and the larva apparently feeding, the ciliation of the median portion of the posterior half of the velum seems to act towards and into the mouth, and I am inclined to think that the very act of swimming itself tends to sweep diatoms and other food particles into the mouth. I have sections showing long cilia of the anterior face of the folded velum pointing backwards into the mouth, and I have noticed in living larvæ the posterior part of the rim of the mouth projected forwards below, so that the hollow vertical crease of the velum led back into the open œsophagus. From a consideration of the size of the velum in the larva and the size of the smallest recognizable palps in the spat it would appear that the velum would have to suffer a period of decay, followed by a period of vigorous growth. Restricting one's observations to the oyster it might seem more likely that the lower palps should originate from the foot and only the upper ones from the velum. The foot is ciliated and has a median ventral furrow corresponding with the division-line between the lower palps. In that case we would expect to find supra-œsophageal ganglia in the bases of the upper palps, in front of the œsophagus, as well as vestiges of pedal organs (pedal ganglia, otocysts) in the bases of the lower palps, behind the œsophagus. But in my sections I have not been able to recognize these structures, and reflection on other bivalves, where both foot and palps persist as functional organs in the adult (clam, mussel, &c.), proves beyond doubt that the foot has nothing to do with the lower palps.

In the face of the above mentioned difficulties it may be questioned also whether the velum has anything to do with the palps. In some cases larvæ with the velum protruded and partly severed from the body may be seen, as well as completely separated vela, still capable of muscular and ciliary swimming movements. This suggests the possible atrophy and dehiscence of the organ, such as was asserted by Davaine but declared by Ryder as not having been confirmed by any other observer. I can confirm the observation, but I do not regard it as conclusive. Such cases may result from the accidental pinching off by a snapping closure of the shell-valves. The small size, shrunken appearance, enfeebled movements, and even the accident itself point towards an antecedent loss of ability to respond correlatively to the activity of other organs such as the contraction of muscles and closing of the shell. In certain free-swimming larvæ, that may be old and perhaps belated in their efforts to become attached, the velum can be observed to suffer reduction in size and vigour. This would seem to point to a natural decay of the organ, that might be followed by complete resorption.

In this connection may be mentioned the young spat obtained and figured by Jackson (1890, Plate XXIV, figs. 1, 2). He states "A large, lobed, ciliated velum still exists. .. .. ..The long vibrating cilia were in active motion and some motion of the velum as a whole was noticed; but it was not seen to extend beyond the margins of the shell." This is the stage upon which Jackson's original work began. If he had known the free larva immediately preceding fixation he would have recognized at once that the velum in his spat was not "large" but reduced, and doubtless also that the activity of the velum and of the cilia was likewise becoming arrested. In fact he did not notice that in 24 hours the velum had disappeared.

Of the thousands of larvæ at one's disposal in plankton it may occur that relatively few show a disposition to swim, creep, or otherwise exhibit their soft parts in activity. Under such conditions it is not safe to build too much on the small number of observations of dehiscence or of reduction. I have therefore attempted to make observations on what I felt sure were normal and healthy individuals, immediately before, at, and closely after fixation. The size, depth, overlying of organs, presence of pigment, absence of movements under the unnatural conditions of a

microscopic preparation, render it very difficult to obtain satisfactory views in the living state. I have selected preserved specimens, made sketches of them and taken measurements, and then prepared series of sections of them, of full grown larvæ that must have been on the point of becoming fixed, of recently attached spat that were smaller than, the same size as, or scarcely larger than the largest larvæ, and succeeding stages up to sizes big enough for dissection. I have sections of seven larvæ varying about a length of 55, and spat of lengths 53 (=·365 mm.), 55 (=·379 mm.), 55, 55, 60, 62, 65, 67, 70, 72, (=·496 mm.), 80, 105, 110 (=·759 mm.), 110, 115, 145, (=1 mm.) and the following lengths in millimetres: 1, 1, 1·5, 2, 2, 2·5, 3, 3, 3·5, 4, 5, 5·5, 10·5, 21, 32, 47. One would think that with this preparation the subject could be easily settled, as many a subject might be, but those used to studying series of sections know that with such minute objects there are great difficulties, one of which is the obtaining of the sections symmetrically or in the required direction. Besides, other complications arise that are not observable in living specimens. Such a question as "Does the velum become changed into the palps?" becomes rather "Does any part of the velum furnish a starting point for the production of palps?" The palps are oral organs and the mouth is but the open end of the œsophagus, which latter is bound up with the velum, being moved with it and associated with it in some of its activities. The tissues between the œsophagus and velum are common to the two, and it becomes difficult to decide to which they belong.

A spat of length 53 (=·365 mm.) has still the structure of the larva, and as such possesses a distinct velum (Plate VI, Figs. 11, 12), which was not rejected bodily at the time of fixation. It is, however, somewhat shrunken, collapsed, and of a vague structure, such as would suggest loss of function. At a size of 55 the velum is so far gone as to be unrecognizable, and at 62 there remain mere vestiges of it, chiefly of its muscles. It is surprising how rapidly it disappears, for this small growth of spat can represent but a few hours—a day at the most. The chances are that the change is generally more rapid, for the spat of 55 length must be an unusually young one, so that its velum may still have had a short lease of life when fixation took place.

While dealing with the fate of the velum and its relation to the palps it might seem best to consider also the origin of the palps, since it is not only necessary to prove that they are not transformed velum, but also, as an additional proof, to show what they do spring from. But as they more properly belong to the mouth their origin will be taken up with the intestinal system.

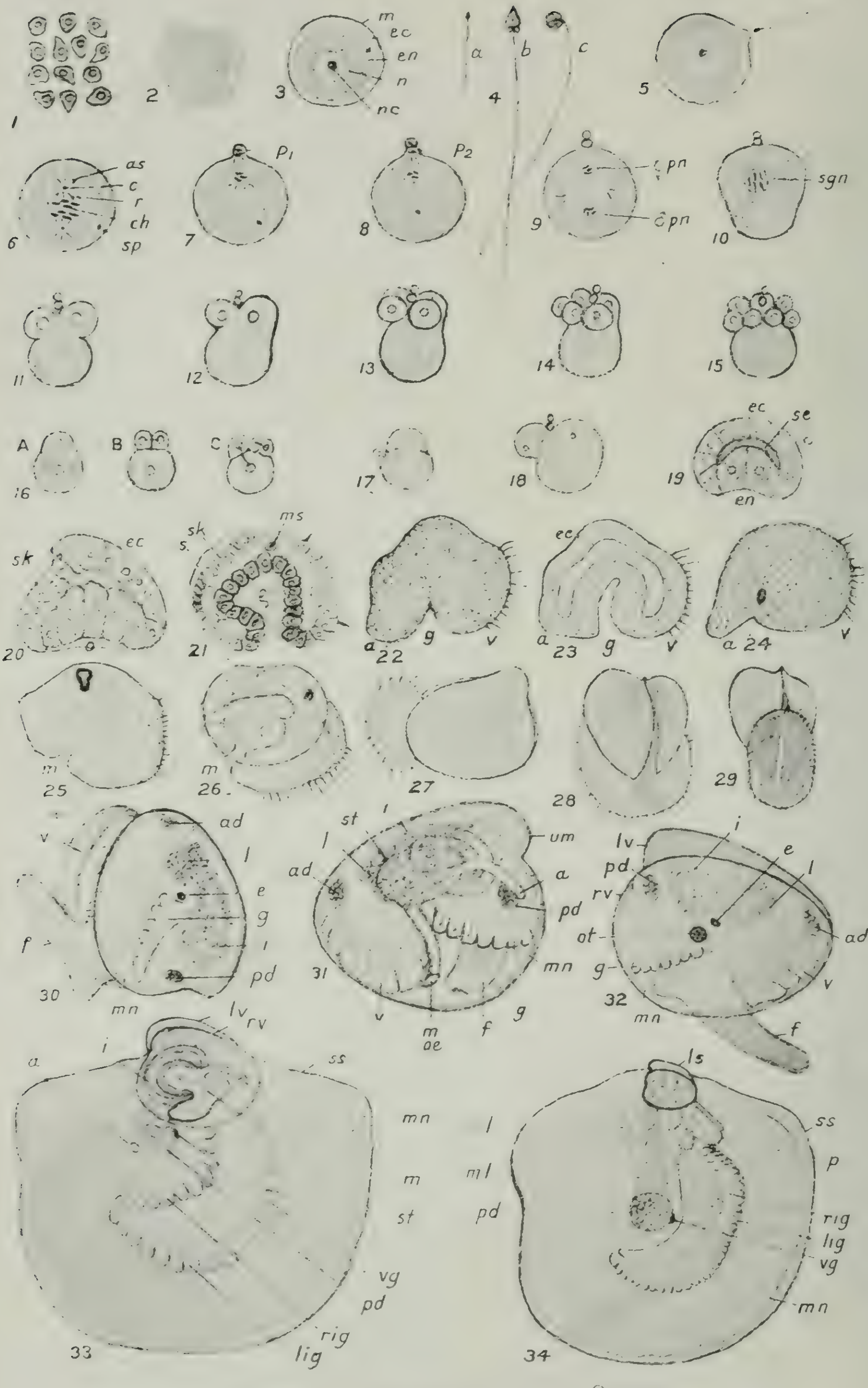
The Foot persists into young spat stages, in which it may be followed, in sections, to spat beyond 1 mm. in length. In the sections of my youngest spat (which was scarcely over $\frac{1}{3}$ mm. in length) it is present in undiminished size (Plate VI, figs. 12, 13, 14), though not so clear and definite

in structure as in the full-grown larva. In a spat of ·44 mm., in which the foot was cut longitudinally, it is shrunken until the lateral walls of the distal half are near together and the long cilia stand out in shaggy clusters. In one of ·79 mm. (Plate VI, figs. 27, 28), it is reduced to a small, ventrally grooved mass, below and behind the mouth and between the bases of the inner palps, in which condition it may be traced until it gradually flattens out and thins into the integument of this region.

Both velum and foot are functionally at their best at the time of fixation. Immediately after this they rapidly dwindle until they have completely disappeared, not even leaving a trace of any of their contained organs, such as supra-œsophageal and pedal ganglia, otocysts, and byssus gland.

Method of Fixation: Byssus Gland.—Fixation takes place at the end of larval life, and is the one thing which distinguishes the late stages of the full-grown, free-swimming or free-creeping, well organized larva from the young stages of the similarly constituted but attached spat. Any of the soft parts, as velum, mantle, or foot, have a tendency to cling to objects against which they press, and larvæ of all stages are liable to be found temporarily resting in such a condition. But this is not permanent, and is not what is meant by fixation in this work. The soldering of the left valve of the shell fast to a solid object of support is a process for which preparation has had to be made in the organism—preparation not only for the material used but for the ability to apply it. I had formerly supposed that fixation was accomplished in an easy and natural way, and almost as a matter of course, by the deposit of the new calcareous material of the first growth of the spat shell at the edge of the left valve of the larval shell, and uniting it at the same time with the object upon which it rested.

In the preparation of sections it is necessary to decalcify the shells of the specimens before they can be cut. Sections of young spat show on the outside of the left valve a layer which does not occur on the right valve, and which is of a different appearance from the matrix of the calcareous shell. It is somewhat homogeneous or faintly striate and has rather a horn colour, with some tendency to receive staining matter, while in the spat shell the calcareous matter is dissolved out leaving only the thin outline of the periostracum or other organic matter. In my youngest spat of very recent fixation (Plate VI, fig. 10, c) this layer has a thickness of ·055 mm., while the remnant of the shell elsewhere is an irregular line not more than one-eighth as thick. This spat was caught on a strip of window glass and afterwards broken away clean, leaving no chance for carrying away any part of the substratum. The fixation material had been spread over rather more than half of the left valve of the larval shell, beginning almost at the anterior edge, extending almost to the umbo, but falling short posteriorly. On these



STAGES IN DEVELOPMENT OF THE OYSTER
Diagrams Showing the Growth of the Various Organs from Egg to Spat Stages

KEY TO PLATE V

Fig. 1. Oyster ova, under low power, magnification 50 diameters.

Fig. 2. Oyster sperm, under low power.

Fig. 3. Ovum, under higher power, magnified 250 diameters, *m.* membrane; *ec*, ectoplasm; *en*, endoplasm; *n*, nucleus; *nc*, nucleolus.

Fig. 4. Spermatozoa, *a*, magnified 250; *b,c*, magnified 1,000 times.

Fig. 5. Ovum and spermatozoön about to meet prior to fertilization.

Fig. 6. After entrance of the spermatozoön into the ovum. *as*, astrosphere; *c*, centrosome; *r*, rays of the spindle; *ch*, chromosomes; *sp*, head of spermatozoön.

Fig. 7. Extrusion of first polar body, p_1.

Fig. 8. Second polar body, p_2.

Fig. 9. ♀ *pn*, female pronucleus.
♂ *pn*, male pronucleus.

Fig. 10. *sgn*, segmentation nucleus.

Fig. 11. First cleavage.

Fig. 12. Resting stage.

Fig. 13. Second cleavage.

Fig. 14. Third cleavage.

Fig. 15. Fourth cleavage.

Fig. 16. Diagram of cleavage from Korschelt and Heider, Part IV., fig. 11.

Fig. 17. Horst's fig. 3.

Fig. 18. Brooks' fig. 14.

Fig. 19. Median sagittal plane to show the process of invagination. *ec*, ectoderm; *en*, endoderm; *sc*, segmentation cavity.

Fig. 20. Horst's fig. 8 turned upside down to bring the blastopore, *o*, below, and the preconchylian (shell) gland, *sk*, above. This is a later gastrula than fig. 19.

Fig. 21. Horst's fig. 13 rotated to the same position as the other figures for ease of comparison. *g*, gastric cavity; *ms*, mesoderm; *s*, shell. The gastrula shows also ectoderm, shell-gland, cilia of velum, endoderm, blastopore, segmentation cavity.

Fig. 22. Brooks' fig. 32. Surface view of embyro (larva) from right side.

Fig. 23. Brooks' fig. 33. Optical section of preceding (compare with fig. 21).

Fig. 24. Brooks' fig. 36. Beginning of shell-valve, down on near side.

Fig. 25. Brooks' fig. 37. Beginning of shell-valve, up on near side

Fig. 26. Brooks' fig. 44. Right side of embryo (larva) si-

The oldest stage raised by Brooks. Compare Pl. I, fig. 12.

Fig. 27. Much older larva (umbo-stage) from the left side, swimming. Not equally magnified with preceding. (Compare Pl. I, fig. 16).

Fig. 28. Similar larva with velum flattened against slide, viewed from behind.

Fig. 29. Similar larva, viewed from the front.

Fig. 30. Full-grown larva (compare Pl. I, fig. 20), from left side; anterior end tilted up, valves of shell opening for protrusion of velum (*v*) and foot (*f*). Through the left valve can be seen the gill (*g*), pigment-spot (*e*), liver (*l*), intestine (*i*), anterior and posterior adductor muscles (*ad*, *pd*), and edge of mantle (*mn*).

Fig. 31. Full-grown larva, from left side: *ad*, *pd*, anterior and posterior adductor muscles; *v*, velum; *f*, foot; *g*, gill (left inner hemibranch); *mn*, mantle; *m*, *oe*, mouth, œsophagus; *st*, stomach; *l*, liver; *i*, intestine; *a*, anus; *um*, umbo.

Fig. 32. Full-grown larva from right side—the position in which it becomes attached. *ad*, anterior adductor; *pd*, posterior adductor; *rv*, right valve; *lv*, left valve; *i*, intestine; *e*, pigment spot; *l*, liver; *v*, velum; *f*, foot; *mn*, edge of mantle; *g*, gill (right inner hemibranch); *ot*, otocyst.

Fig. 33. Spat of 1 mm. length (compare Pl. II, fig. 5) *lv*, left valve of the larval shell; *rv*, right valve of the larval shell; *ss*, spat shell; *mn*, mantle; *m*, mouth; *st*, stomach; *vg*, visceral ganglion; *pd*, posterior adductor muscle; *rig*, right inner hemibranch (same as *g* of fig. 32); *lig*, left inner hemibranch (same as *g* of fig. 31); *a*, anus; *i*, intestine.

Fig. 34. Spat of 2 mm. length (compare Pl. II, fig. 7); *ls*, larval shell; *ss*, spat shell; *p*, palps; *rig*, right inner hemibranch; *lig*, left inner hemibranch; *vg*, visceral ganglion; *mn*, mantle; *pd*, posterior adductor muscle; *ml*, line along which the muscle travelled in the growing spat; *l*, liver.

Diagrams Showing ...

accounts I judge that the fixative was an organic secretion of different origin from both larval and spat shells.

There can be little doubt that the larval and spat shells are built by the apposition of new matter at the growing edges, and that this matter is secreted from glands situated in the thickened margins of the mantle. Whether they are secreted from the same set of glands in both cases is more than doubtful. Thin margins of the protruding mantle, as well as prepared sections show more or less elongated unicellular glands, the larger of which have a narrow neck and an irregular broader fundus, containing a refringent semi-fluid material. The fixative material represents such a quantity of matter that it could scarcely be produced quickly enough by the same means as that of the shell. Besides there would be an insurmountable difficulty in the bringing of the mantle margins far enough outside of the shell to be applied to the proper spot. Fixation is no haphazard process. Such a sudden change in the mode of existence of the organism, occurring with regularity at a definite period in the life of each individual, can not have failed to call out a correlative organization, permitting accommodation to a new method of living.

Turning to the oldest larval stages, immediately preceding fixation, I find a gland, the byssus gland, capable of supplying secreted matter, that might be used in fixation, and, at the same time, situated in an organ, the foot, capable of bringing the mouth of the gland in the heel to the proper spot on the outside of the shell. The usefulness of the foot as an organ of locomotion, as a clinging organ, as an organ of fixation, had appealed to me for some time, but I had no direct evidence to support the view that it was really the organ of final attachment. Upon observing the soldering matter on the outside of the left valve of the lately fixed spat, however, the conclusion became irresistible. Re-examining the byssus-gland I find that it occupies in full grown larvæ a considerable portion of the inside of the foot (Plate VI, figs. 4, 5), and consists of a median and two lateral lobes, with a main duct running through the median portion and continuing to the external opening at the end of the heel. The cells are large and distended with a transparent secretion, which presses the small nuclei towards the walls. In the youngest spat, on the other hand, the byssus-gland is relatively inconspicuous and its cells shrunken and collapsed.

As to the method of applying the cementing substance, the presence of a little hook or knob of secretion (Plate VI, figs. 11, 16), near the upper anterior edge of the shell, gives a hint that, while the larva is lying upon its left valve, the foot is thrust forwards and upwards until the point of the heel, on which opens the duct of the byssus-gland, comes to this spot, and then the secretion is poured out, flowing between the shell and the substratum, until fully discharged, when the withdrawal of the foot, breaking the current of the outflow, leaves the detached end of the hardening se-

cretion as a tapering point which falls over, making a hook-like or knob-like process.

Succeeding stages show that the gland suffers rapid degeneration after the completion of its work. Later and larger stages of the spat must increase the surface of attachment by a different method, viz., by the same means and at the same time as the growth of the shell.

Ryder (1882 p. 283) attempted to discover the way in which the larva attaches itself, and was misled by confining his attention to straight-hinge stages, adhering as nearly as he could make out by the edge of the protruding mantle. He supposed that this was the normal manner of first becoming adherent, and that afterwards the attachment was made firm by the building of a few layers of shelly matter along the edge of the lower valve.

Horst (1884, p. 907) also observed a little band of secondary shellsubstance, secreted along the edge of the shell of the larva, which he says may possibly have aided the little oyster in adhering, but regrets that he was unable to solve the problem satisfactorily.

Huxley (1883, p. 113) in like manner states: "When the free larva of the oyster settles down into the fixed state, the left lobe of the mantle stretches beyond its valve and applying itself to the surface of the stone or shell, to which the valve is to adhere, secretes shelly matter, which serves to cement the valve to its support."

Rice (1883 p. 28) wrote: "Further observation seems to show that this is their normal mode of attachment, that is, to thrust out the velum from between the shells and adhere to whatever is within reach, afterwards the animal falls over to one side, generally the left, and the shell of that side gradually forms around and out beyond this attachment of the young animal."

Jackson (1900 p. 303) says that "The preliminary fixation is probably effected by means of the reflected mantle border, as described by Ryder, and is then immediaately succeeded by a cementing conchyolin attachment of the extreme edge of the lower left prodissoconch valve."

Regarding the presence of a byssus, *Ryder* ('82 p. 383; '82-'83, p. 329; '84 p. 758) was doubtful. *Horst* believed that he had noticed a small byssus.

Jackson ('90 p. 302-3) reasoned that "As the byssus is an organ developed in the ventral portion of the foot, the high reduction or almost complete absence of that organ is in itself strongest evidence against the suggestion that the attachment of the young oyster is effected by means of a byssus of however short a duration . . . . In view of the evidence it is therefore safe to conclude that the oyster does not have a byssus at any period of its development."

The Mantle, in living spat, may often be seen protruding beyond the edges of the shell-valves, but in preserved specimens it is retracted, sometimes close up to the gills and body, so that the soft parts of the animal may occupy a half to a third of the cavity of the shell. In even the youngest stages the margins of the mantle are thickened and have longitudinal grooves and short tentacular processes (Plates VI and VII). It is these thickened margins that contain numerous unicellular glands, doubtless for secretion of the substances of the shell. Under the hinge there is a special pad of gland cells for secretion of the hinge-ligament. Differences in the two halves of the mantle afterwards become noticeable, such as thickness, length, and the greater freedom of the right side, where, for a considerable area in front of the adductor muscle, there is open communication from the supra-branchial chamber to the outside at the dorsal edges of the mantle (Plate VII, fig. 14). Anteriorly the right and left margins grow together for a distance, making a sort of hood in front of the mouth.

Adductor Muscles, at the time of fixation (Plate V, figs. 30-32)) are of nearly equal size, the anterior being perhaps a little larger than the posterior. But from this time onwards their history is different. The anterior adductor becomes smaller, is moved upwards and backwards from its original position, and finally it is crowded to the edge and disappears. In my sections distinct transverse fibres can only be traced as far as to the spat of 72 units ($=\frac{1}{2}$ mm.) The posterior adductor, on the other hand, increases regularly in size and moves downwards and slightly backwards, leaving distinct lines on the inside of the shell to indicate its change of position (Plate V, fig. 34). In the newly attached spat it is situated in the prodissoconch, just below the hollow which separates the umbos from the projecting posterior end of the shell. In spat of ·5 mm. it is half way between this and the lower edge of the prodissoconch. Spat of ·85 mm. show it moved on to the dissoconch just below the edge of the prodissoconch, and those of 1.5 mm. have it the depth of the prodissoconch, below the lower edge of the latter. In all stages it is about half way between the dorsal and ventral edges of the shell, and slightly behind the middle in the antero-posterior direction. The movement may be effected by a slow creeping of the muscle, perhaps due to downward pressure from the growth of the body above, or by the addition of new fibres below and the absorption of old from above; while the impressions on the shell may result from the inability of the surface of the mantle to deposit new layers of pearly matter under the attached ends of the muscle.

Huxley ('83 p. 112) believed that the adductor muscle of the straight-hinge larva could not be the same as that which exists in the adult, since it lies in the fore part of the body and on the dorsal side of the alimentary canal while the great muscle of the adult lies on the ventral side of the alimentary canal, and in the hinder part of the body.

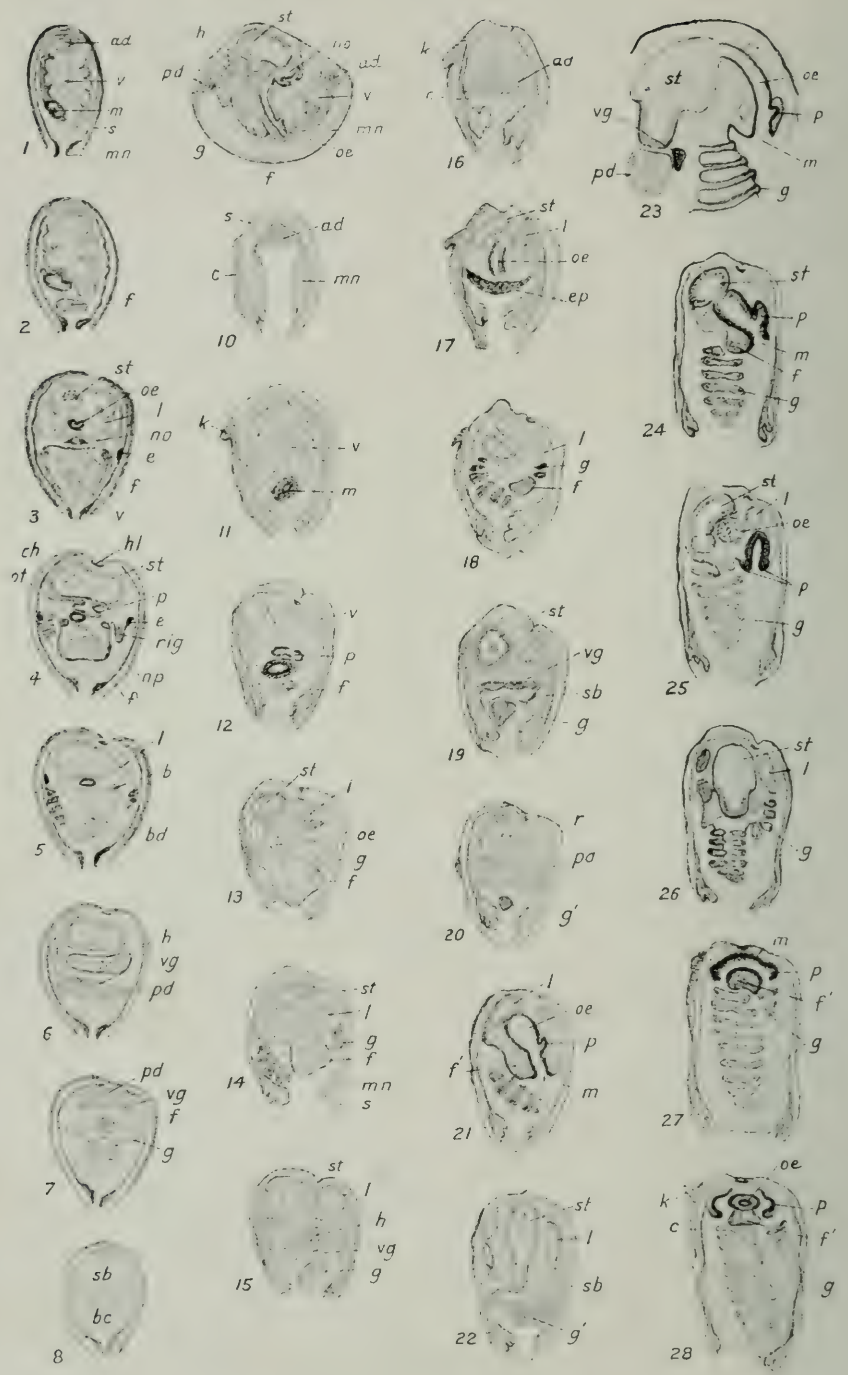
Jackson (1888) discovered in his young spat that there are two adductor muscles —the anterior adductor as seen by Huxley, and another, the posterior adductor— the same as occurs in adult dimyarian Pelecypoda. The posterior adductor persists as the great adductor of the adult oyster.

Gills, at fixation, are present in essentially the same condition as already described for the full-grown larva (Plate V, figs. 30-32). There are two—one on each side—attached laterally between the foot and the mantle (Plate VI, figs. 4, 5, 13, 14). Each may be compared to a comb having its back (the attached axis of the gill) turned upwards and its teeth (the gill filaments) turned downwards. The axes slant downwards and backwards past the foot, joining behind (Plate VI, figs. 7, 22), and the filaments in this region are short and incompletely separated. In sections of the spat there is a noticeable difference between right and left gills—the left being largest and most advanced in development (Plate VII, fig. 4). New filaments begin as mere knobs partially split from the posterior mass, the splitting proceeding from the outside and from below but never complete above, where all the filaments remain connected in the axis. In the larva, immediately before, and in the spat, immediately after fixation,

there are about eight filaments, but when the spat reaches .86 mm. in height there are about sixteen comparatively long filaments on the left side and about ten shorter filaments on the right side—the left gill extending in front of and behind the right one and occupying most of the branchial chamber. In a spat of 1.5 mm. height I counted twenty-three filaments and in one of 3 mm. fifty filaments in the left gill. In spat of 2.5 mm. height there appears on the right side (Plate VII, fig. 14), outwards from the already present gill, a third series of minute, papilla-like filaments, and when the spat reaches 3 mm. in height a fourth series (Plate VII, fig. 15) is to be seen in the corresponding position on the left side. They increase in size during the growth of the spat until the animal possesses four complete gill-leaves, corresponding with those of the adult—two inner, which began to develop in the larva, and two outer, which did not originate until after entering on the spat stages.

During larval development the gills make but little progress towards the complicated structures they possess in the adult. The free-swimming larva being small, respiration can for a time be largely subserved by the surface, of which velum, foot, mantle and gills form a large part. But fixation effects a marked change in the mode of living and is followed by far-reaching modifications in the organization of the spat. The animal economizes by discarding such active muscular and sensory organs as the velum and the foot, but finds some disadvantage in the matter of aëration, resulting from the loss of movement and of surface. Both of these disadvantages are met by the increased surface and ciliation of the gills. Moreover, as the animal no longer comes in contact with its food through swimming movements, it must depend upon the respiratory currents for bringing food to itself. Hence the gills acquire the double importance of acting as the chief organ of respiration and at the same time of serving as a gatherer of food. Under this simple arrangement the growth of the organism is rapid and its development hastened to completion. At the same time, since the conditions favourable to bilateral symmetry are interfered with at fixation, the equal balancing of right and left sides in the further growth of organs must be left to heredity. But gravitation, i.e. weight and pressure, acting unequally upon the two sides, soon effects a marked difference; the left, now under, gill grows much faster than the right, now upper, one, so that there is more room and less pressure above, facilitating the development of the right outer gill-leaf before the corresponding one of the left side. Irregularity also soon becomes noticeable in the higher level of origin of those of the right side, and in a tendency towards a radial symmetry of these organs with reference to the posterior adductor muscle.

In the youngest stages of the spat transverse sections of the filaments show each of the larger ones to be flattened by pressure antero-posteriorly and extended laterally, sometimes rather wedge-shaped, with the broad



SECTIONS OF LARVAE AND SPAT

KEY TO PLATE VI

Figs. 1–9. Sections through full-grown oyster larvæ: 1–8, transverse; 9, median sagittal. All the transverse sections are looked at from behind, so that dorsal is above and left is on the observer's left. Their position should be located on fig. 9 (or by comparison with Pl. V, figs. 30, 32). Easily recognizable parts are generally indicated where they first occur and sometimes not afterwards.

Fig. 1. Section across the anterior end (6th of a series of 32 sections): *ad*, anterior adductor muscle; *v*, velum; *m*, mouth; *s*, shell; *mn*, border of mantle.

Fig. 2. Second section behind the preceding in the same series: *f*, tip of foot.

Fig. 3. Section of another series (slanting downwards and forwards): *st*, stomach; *oe*, œsophagus; *l*, liver; *no*, supra-œsophageal nerve commissure; *e*, pigmentary eye-spot; *p*, rudiment of palps; *v*, velum. (Above the velum on a level with the eye-spot is a crumpled layer of chitin extending crosswise; above the eye, next to the mantle, is a retractor muscle of the velum.)

Fig. 4. Section of same series as 1 and 2 (14th of the series, slanting slightly down and back. On account of the asymmetry of the larva, and also on account of the difficulty of orientation the two sides are not quite alike.) *hl*, hinge ligament; *st*, stomach; *p*, rudiment of palps above (in front of) the œsophagus; *e*, eye-spot; *rig*, right gill (what becomes the right inner hemibranch of the adult gill). The left gill is larger than the right and its filaments were slanting so that three were cut across; *np*, infra-œsophageal or pedal commissure; *f*, foot; *ot*, otocyst (right one also showing); *ch*, chitin in the crease between velum and body.

Fig. 5. Section 17 of the series; *l*, liver; *b*, blood vessel; *bd*, duct of the byssus gland in the heel of the foot (in Fig. 4 it is cut across and in each side are some follicles). Part of the stomach, the œsophagus near where it enters the stomach, one eye-spot and the gills are also shown.

Fig. 6. Section 23 of the series: *h* heart containing blood-cells; *vg*, visceral ganglion; *pd*, posterior adductor muscle. Stomach and lobe of liver showing.

Fig. 7. Section 16 of same series as Fig. 3. *pd*, posterior adductor muscle; *vg*, visceral ganglia; *f*, heel of foot; *g*, gills of opposite sides uniting behind foot.

Fig. 8. Second section behind preceding: *sb*, supra-branchial chamber; *bc*, branchial chamber.

Fig. 9. Median sagittal section through larva. The velum and foot are withdrawn tightly up against the body and partly turned sideways.

st, stomach; *no*, supra-œsophageal nervous system; *ad*, anterior adductor muscle; *v*, velum; *mn*, border of mantle; *oe*, œsophagus; *f*, foot; *pd*, posterior adductor muscle; *h*, heart.

Figs. 10–15. Transverse sections from a series of 30 through the youngest oyster spat (compare Pl. II, fig. 1). This spat, caught on a strip of glass, was actually smaller than the oldest larvæ of the preceding sections. It measured 53 (53 x 6·9 = ·36 mm.), while they measured 55. There had not been the slightest growth of shell since the attachment, but the left valve is thickened by byssus cement which is not to be found on the right and is not dissolved away by decalcification.

Fig. 10. Section 2 of the series: *s*, shell; *c*, cement; *ad*, anterior adductor muscle; *mn*, mantle.

Fig. 11. Section 8 of the series: *k*, knob or drop of cement; *v*, velum, still present in the fixed spat; *m*, mouth.

Fig. 12. Section 10 of the series:
p, rudimentary palps, between velum and mouth; *f*, tip of foot.

Fig. 13. Section 14 of the series:
st, stomach; *l*, liver; *oe*, œsophagus; *g*, gill; *f*, foot.

Fig. 14. Section 17 of the series: stomach, two lobes of liver, right and left gills, foot, mantle, and shell.

Fig. 15. Section 23 of the series: stomach, two lobes of liver, heart with blood, visceral commissure, posterior undivided knob of gill axis.

Figs. 16–20. Sections 5, 8, 13, 20, 23 through a spat of length 60 (= ·41 mm.). Compare Pl. II, fig. 2; *ep*, high epithelium in region of mouth; *r*, rectum. The velum is gone and the foot greatly reduced.

Figs. 21–22. Sections 5 and 15 through spat of length 72 (= ·49 mm.). Compare Pl. II, fig. 3. The mouth is twisted to the right (upwards).

Fig. 23. Part of two sagittal sections of a spat 105 in length put together.

Figs. 24–26. Sections 8, 9, 10 of a spat 110 length (= ·75 mm.). Compare Pl. II, fig. 4. The mouth is twisted to the right (upwards) and shows the mode of origin of the upper and lower palps of that side. The left gill (left inner hemibranch) is partly split into outer and inner (lower and upper) lamellæ. In 26 the smaller right gill unites with the larger left one.

Figs. 27–28. Sections 5 and 6 of a spat of 115 units (= ·79 mm.). The mouth and palps are not twisted out of position or grown upwards towards the right side. The foot is shrunk to form only a muscular ridge along the abdomen. The left valve of the shell is damaged, as often happens in separating the spat from the object on which it is fastened.

end outwards. Each is composed of a surrounding row of epithelial cells close together, so as to leave no or scarcely any lumen, with sometimes a few small connective-tissue cells. In spat of 60 units length some of the filaments have become very broad from side to side, and their anterior and posterior walls approach each other in the middle as if to constrict into outer and inner halves, connected by a narrow transverse bridge. The outer and inner edges are similarily modified, and the parts each side of the constriction are formed alike. Spat of a length of 67 have some of the filaments of the left gill constricted in two, and it is possible to recognize the frontal epithelium and respiratory cilia, the supporting rods and tissues and small lacunæ. In spat of 110 units this is carried so far that the gill is imperfectly split into outer and inner lamellæ, the outer and inner halves of each filament being widely separated above, but remaining connected below (Plate VI, fig. 26). Anteriorly the inner lamellæ of the two gills approach each other, towards the median ventral line of the abdomen, where they are attached, but behind this they unite, separating off a supra-branchial chamber above from an infra-branchial chamber below, the supra-branchial chamber dipping down between the two lamellæ of each gill. Posteriorly this is extended by the formation of new filaments, which push the older ones forwards along the growing abdomen, each new filament developing in the same way as the preceding, so that the lamellæ of a gill are united not only along the ventral edge but behind as well. Water from the infra-branchial chamber passes through the slits between the filaments, into the inter-lamellar spaces, and up into the supra-branchial chamber, from which it can escape posteriorly. These slits, with the growth of the gills, come to be interrupted by inter-filamentar junctions, that divide them into ostia. The spat of length 60 already has a row of such junctions, connecting the tips of the filaments of the left gill. In some cases these appear to have persisted from the first. In a similar manner, during the splitting of the filaments in the formation of outer and inner lamellæ, the separation is often incomplete, leaving bridges of inter-lamellar junctions. Inter-filamentar and inner-lamellar junctions help to support and hold in place the delicate net-work of the increasingly large and complex branchial apparatus. With growth in length the axes come to curve downwards and backwards, as if doubling round the great adductor muscle, so that the anterior filaments project forwards, but the posterior ones ventralwards, and vertical transverse sections of the spat cut the anterior filaments transversely, but the posterior ones longitudinally. When the right and left outer gill-leaves develop they run through a similar history, the upper edges of their inner lamellæ becoming connected with the corresponding outer edges of those already in existence and the upper edges of the outer lamellæ becoming connected with the mantle.

The foregoing account of the apparent ontogenetic development of the gills of the oyster differs markedly from the recorded phylogentic development of the gills of lamellibranchs. This difference, like the asymmetry of the prodissoconch, may be understood as a cænogenetic modification of biogenesis—a sort of short-cut to the final structure.

Note on the Phylogeny of the Lamellibranchiate Gill.—For a long time it has been customary among zoologists to speak as if the oyster or other bivalve mollusk, possesses four gills, which it really appears to do, two on each side of the body. Comparative anatomy and comparative embryology of the different classes have led to the view that bivalves have been developed from a primitive, symmetrical, gastropod-like ancestor, having a simple head in front bearing two tentacles, two eyes, and a mouth with a rasping tongue; a low conical shell above, that could be drawn down over all the soft parts, and lined by a mantle that secretes its material; a flat, creeping and clinging foot below; and two feather-shaped gills, disposed right and left, projecting backwards. Each of these was a symmetrically constructed, bi-pectinate gill or ctenidium, having a central axis with two rows of filaments, an upper and a lower. There are still living, limpet-like gastropods along our coasts possessing such characters, although no one species retains them all or in the most primitive form.

The class of mollusks to which the oyster belongs has in the course of time suffered modifications of the characters mentioned. Its members have taken to a more quiescent mode of life, such as burrowing in sand or fixing to rocks, and in consequence have largely lost those external organs of locomotion, plunder, and special sense, so necessary to free-roving animals. The absence of a head has been regarded as characteristic (hence the class has been called Acephala); in place of a single piece they have developed a shell with two valves (Bivalva); the foot in by far the greatest number of forms has become somewhat hatchet-shaped (Pelecypoda); the gills are leaf-like, each separable into flat plates (Lamellibranchia). If all bivalves had become equally modified it would certainly have been difficult to determine the origin of the group, but owing to the diversity of natural conditions and the reactions of these upon living organisms, certain species have been forced to pursue special lines of action in order to better their chances for life, with the result that the organs chiefly concerned have become more specialized, while other organs have retained much of their original structure, and it is just these latter that are especially valuable in tracing ancestral affinities. As long ago as 1848 Lenckart comprehended the unity of structure in the gills of Mollusca, and his views have been supported by Menegaux, Pelseneer, and many others. Peck has studied the Lamellibranch gill. Lankester, Hatschek, Thiele, Lang, and others have worked out the phylogeny.

In the adult oyster there is but one gill on each side, comparable with a ctenidium, and composed of two hemibranchs (gill-leaves or branchial foliæ); each hemibranch is split lengthwise, from above nearly to the lower free edge, but not through it, into outer and inner plates (lamellæ), or subdivided transversely into numerous V-shaped filaments of which one-half belongs to the outer lamella and the other half to the inner lamella of the hemibranch. In the full-grown larvæ of the oyster it is possible to recognize the ctenidial axis with its lower series of filaments, but we have to await the spat of 2·5 to 3 mm. to see the upper series, which, it may be conceived, has had to rotate outwards nearly half way round the axis in order to be accommodated within the branchial chamber.

In the course of phylogenetic development the originally straight filaments have become bent upon themselves to permit of greater length (breathing surface) and still be protected in the branchial chamber—those of the ventral series were folded inwards and those of the dorsal (but now lateral) series were folded outwards, while their tips, coming in contact with the foot in the one case or the mantle in the other, clung for support, were directed upwards, and finally became united along the side of the body or along the inner surface of the mantle. At places their ciliated surface became knit together for further support (inter-filamentar and inter-lamellar junctions), leaving intervening gill-slits between contiguous filaments and ascending water-tubes between opposed lamellæ. At the level of union of the gill-filaments with the body and with the mantle, they separate off a branchial chamber below and between the suspended hemibranchs from a supra-branchial (or cloacal) chamber above, and by the activity of the cilia, water is drawn into the former, directed through the gill-slits, up the water-tubes, and out by the cloacal chamber. The position of the original ctenidial axis lies above and between the lines of origin of the filaments of each pair of hemibranchs, and is marked

by retaining its connection with the body by a septum carrying blood vessels and nerves.

Ryder ('82, '84, p. 787) wrote: "One of the most conspicuous differences between the symmetrical larva and the young spat is the absence of gills in the former and their presence in the latter."

Jackson ('90, p. 301, 303-306) knew the gills from the youngest stage of the spat, but appears to have had only few specimens. Although particularly interested in phylogeny he made important observations in embryology. The specimen (his Plate XXIV, fig. 4) in which he first recognized the right outer hemibranch was about 5 mm. in height, and must have also had a corresponding left outer one, although it could not be seen. As already stated, all four hemibranchs can be recognized in sections of spat of 3 mm. height. Jackson states that the "ends of the gill-filaments in the spat, Fig. 3, are recurved and joined by concrescence at their tips with the recurved filament tips of the opposed gill-lamella." This is undoubtedly a mistake but one easily made in viewing the specimen from the surface. At the period of Fig. 3, which was a spat of approximately double the height of the prodissoconch, the splitting of the filaments of the left gill would be so complete that it would be an easy matter to follow down one half of a filament and up the other as if it were really reflected. Long before I had prepared sections I had done this but never was quite satisfied at not finding any free recurved tips in the act of becoming reflected as required by theory.

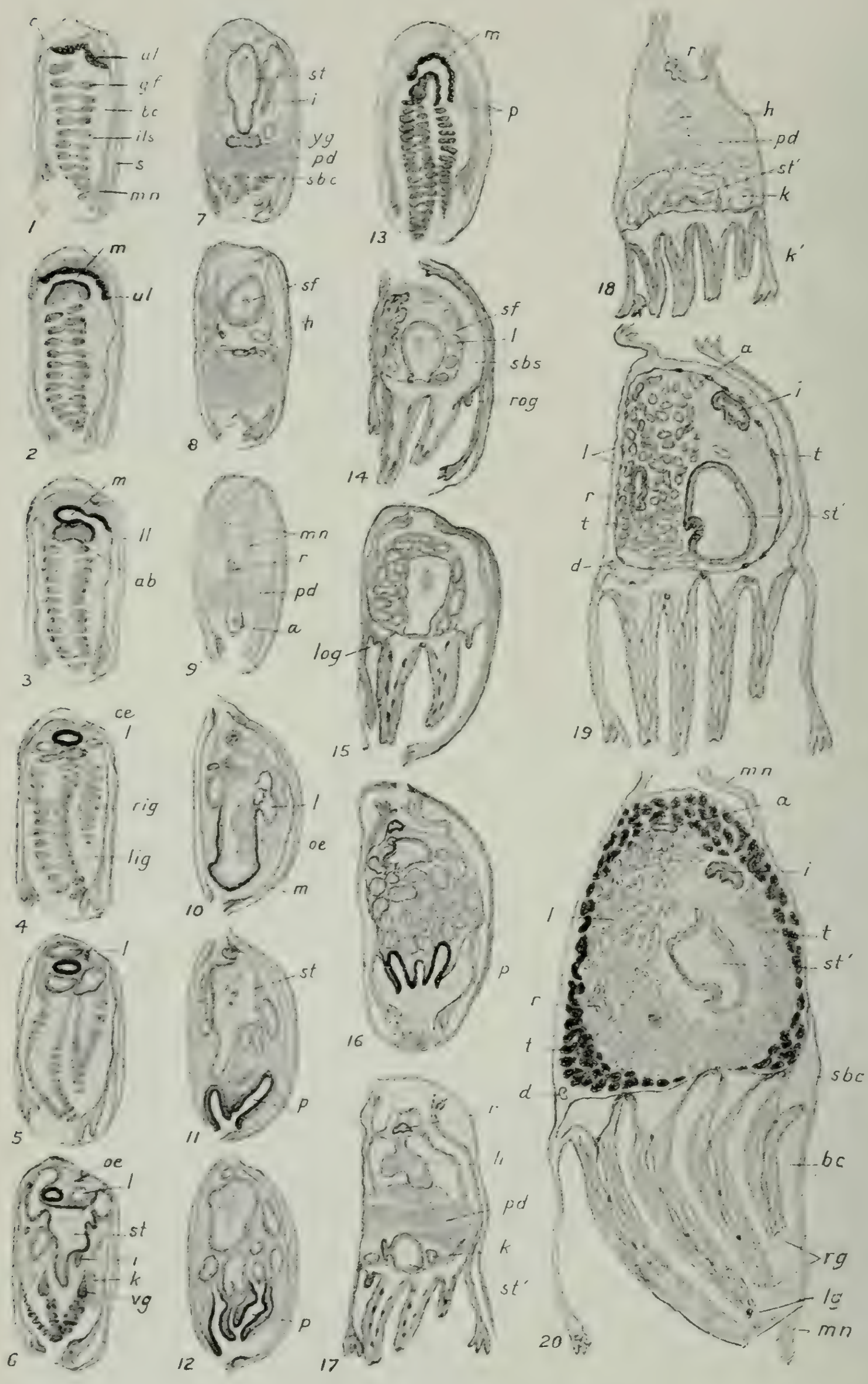
The Intestinal System has all its parts represented in the larva. With the growth of the spat these suffer certain alterations in relative sizes, shapes, and positions. Perhaps the most radical change is produced by a rotation of the body in such a way that the mouth moves forwards and upwards towards the antero-dorsal margin of the prodissoconch, where the anterior adductor muscle used to be. This rotation accompanies and is associated with the loss of the velum, which in the larva is so large as to occupy all the fore-part of the cavity of the shell, forcing the mouth and œsophagus backwards to near the median frontal plane of the body, and causing the œsophagus to be curved backwards around it. In spat soon after fixation, when the velum is completely cleared away, the mouth can occupy its normal position as in the adult. Such a rotation may appear, at first thought, inexplicable, but, when it is remembered that the body of the larva is possessed of great freedom of movement, being at times thrust forwards, putting the retractor muscles on the stretch, it can be readily understood. In fact it is conceivable that these muscles may be made to do duty in bringing about the rotation and in fixing the body in its new position, for after the loss of velum and foot, there is no longer any need of such free movement, consequently these muscles may lag behind other parts in growth, exerting a tension as they do so sufficient to cause the rotation. In harmony with the view of a rotation of the body is the upward movement of the anterior adductor muscle and a downward movement of the posterior adductor muscle, the forward curving of the œsophagus and the more rapid growth of the posterior lower parts of the body.

Mouth and Palps.—The mouth persists from the larva, but, with the taking of its new position and the change in the method of collecting food, there is an attempt at enlarging its capacity. This is partly accomplished by lateral extension, but also by development of palps.

Palps are at first closely allied with the velum, and this is due to the association of the œsophagus and mouth with that organ. The first trace of the organ that can be followed into the palps is found in the larva, in the tissues between the œsophagus and velum. In front of (i. e. above) the œsophagus, and squeezed rather asymmetrically to the right, is a deeply staining, dense band, inclined to be split into two layers by a narrow transverse slit, and also partly constricted into right and left halves (Plate VI, fig. 4, *p*). It appears to be an invagination in front of, and mostly on the right side of the œsophagus, pointing inwards and upwards towards and ending below the supra-œsophageal ganglion. That it does not belong to the velum is shown by the fact that the yellow, chitinous-looking matter, to be found on the surface and in the creases of the upper and more posterior parts of the velum, dips in between this organ and the velum, thus throwing it rather with the œsophagus, with which it remains when the velum disappears. In my youngest spat (Plate VI, fig. 12) this structure is the same as in the larva, excepting that it is rather larger and closer to the end of the œsophagus (mouth). In those a little older (Figs. 21, 23, 24) it doubles across the front of the œsophagus just above the mouth, broadening into a large cavity, that sometimes opens only on the right side. By downward growth of the anterior wall it is made to receive the mouth, and by growth of the inner and outer edges of the opening (Fig. 25) the lower and upper palps are produced. Spat of a length of 72 already show a single furrow on the inner surface of the anterior wall and continuing outwards laterally on to the inner surface of the upper palps. With the loss of the velum the œsophagus comes to curve forwards instead of backwards, and there is need of a broader opening to gather in a greater abundance of minute food-organisms, swept forwards or pushed forwards by the gills, which at this period have grown forwards in close proximity to the mouth. In 1 mm. spat (Plate VII, fig. 1) the two edges of the mantle meet above, forming a sort of hood over and in front of the widely open, transversely crescentic mouth (Fig. 2), that opens a little farther back on the right side than on the left (Fig. 3). The anterior end of the body, between the first gill filaments, where the foot used to be, serves as the posterior (or inferior) support of the mouth, while very short upper and lower palps, possessing only a couple of ridges and furrows, are continuous with the lateral margins of the upper and lower lips and project on each side of the anterior end of the median (left) gill. In 2 mm. spat (Plate V, fig. 34; Plate VII, fig. 13) the palps have increased perceptibly, doubled the number of furrows, turned down, and are seen to be anterior to, but not continuous with, the gills.

Ryder ('82–'84 p. 786) "........it would appear probable that both palps and gills originated from very nearly the same primitive structure..........longitudinal folds of epiblast that were at first continuous."

Rice ('83 p. 28) made an observation which (if we understand proboscis to mean œsophagus) comes curiously near the truth: "During the first period of attachment



SECTIONS OF SPAT AND OYSTER

KEY TO PLATE VII

Figs. 1–9. Transverse sections through spat of 1 mm. length (compare Pl. II, fig. 5 and Pl. V, fig. 33). This is a size sufficiently large to be recognized with a lens.

Fig. 1. Section 17 of a series of 53:

c, cement, of the left valve; *ul*, upper lip of proliferating epithelium; *gf*, gill filament of left inner hemibranch; *bc*, branchial chamber; *ils*, inter-lamellar space (water tube) opening laterally between the filaments by ostia; *s*, shell (right valve); *mn*; thickened tentacular border of the mantle.

Fig. 2. Section 20:

m, mouth; *ul*, upper lip and beginning of palp.

Fig. 3. Section 22:

m, mouth; *ll*, lower lip and beginning of palp; *ab*, anterior tip of abdomen and shrivelled foot. The lips of the right side (uppermost) open farthest back.

Fig. 4. Section 24:

oe, œsophagus (mouth closed in on both sides); *l*, liver; rig, right inner hemibranch; *lig*, left inner hemibranch.

Fig. 5. Section 26: *l*, liver.

Fig. 6. Section 31. The upper of the two lobes of the liver on the left is narrowed at its middle, and in the crease between the two parts, as also between the two lobes, lies a fold of the intestine; *st*, stomach; *i*, origin of the intestine; *k*, kidney; *vg*, visceral ganglion.

Fig. 7. Section 33: *pd*, posterior adductor muscle; *sbc*, supra-branchial chamber.

Fig. 8. Section 39: *h*, heart.

Fig. 9. Section 45: *mn*, folds of the mantle; *r*, rectum; *a*, anus.

Figs. 10–12. Sections of 1·5 mm. spat, slanting downwards and forwards. The left valve was flattened against the shell on which it was fixed.

Fig. 10. Anterior (upper) section: *l*, liver; *oe*, œsophagus; *m*, roof of mouth cavity.

Fig. 11. Second section following, *st*, stomach; *p*, space between outer (upper) and inner (lower) palp of right side. Similarly on the left.

Fig. 12. Second section following. The palps become separate.

Fig. 13. Transverse section through the mouth of a 2 mm. spat: *p*, outer and inner palps of the right side.

Fig. 14. Section of 2·5 mm. spat: *sbs*, supra-branchial slit leading from the supra-branchial cavity on to the dorsal surface; *rog*, right outer

hemibranch. The filaments are cut lengthwise or nearly so in contradistinction to Fig. 13 where they are cut across.

Fig. 15. Section of 3mm. spat. Similar to last but with rudiment of *log*, left outer hemibranch. Both halves of both gills are now represented.

Fig. 16. Section of 3·5 mm. spat just behind the mouth and œsophagus but through the palps (compare Fig. 12).

Fig. 17. Section just in front of the adductor muscle of a 4 mm. spat: *r*, rectum; *h*, heart; *pd*, adductor muscle; *k*, kidney; *st*, descending portion from stomach (compare Fig. 7).

Fig. 18. Section 199 from a series of 307 of a 10·5 mm. spat (the extracted soft parts measured over 7 mm. long and 4 mm. deep); *r*, rectum; *h*, portion of heart; *pd*, anterior fibres of adductor; st^1, descending loop from stomach; *k*, kidney; k^1, nephropore.

Fig. 19. Section 254 from a series of 537 (I stopped sectioning after passing beyond the visceral ganglion) through a 21 mm. spat of which the soft parts measured 14 mm. long and 9 deep. st^1, descending loop from stomach; *i*, ascending portion; *r*, rectum; *l*, liver follicles; *a*, aorta; *t,t*, minute empty follicles of the gonad (testis) which would be unrecognizable but for comparison with more mature stages; *d*, duct (gonaduct) which runs forwards but does not connect at this stage with the gonad.

Fig. 20. Section through the same region of a 32 mm. (nearly $1\frac{1}{4}$ inch) oyster (the soft parts measured 24 x 14 mm.). The follicles of the testis are distended with millions of spermatozoa, the whole gonad staining deeply and standing out in contrast to the rest of the oyster.

when the shell itself is not firmly attached, but simply held firmly down to the substance with which it is in contact, the young animal gets its food, or a portion of it, by means of a sort of proboscis, or elongation of the mouth part, which is capable of being moved about freely within the shell cavity. This proboscis stage lasts until the gills are formed and become of sufficient size to supply food to the animals, when the proboscis, or rather its flexible end, is transformed into the labial palps, which become closely connected with the gill-leaves."

Jackson ('90, pp. 301, 304-305, Plate XXIV, figs. 1–2) mentions palps in the youngest spat stage and fortunately figures them. Long before I had prepared sections of this stage I had decided that palps of such relative size could not be present, and that what Jackson had was nothing but the unrecognized foot. His figures show it immediately behind the already shrunken velum and overlapped by the anterior gill-filaments of both sides. The two transverse lines may have been due to its being crumpled or else already shrunken, and the ventral furrow at the end may have suggested its being double like two palps. It is not the same part as is figured as palps in his figs. 3 and 4.

The mouth narrows down into an *œsophageal tube* of transversely elliptical calibre, lined by ciliated columnar epithelial cells similar to and continuous with those on the palps. The œsophagus is still relatively long and curves over the anterior end of the stomach, passes between the lateral origins of the liver, and enters the stomach from above. The *stomach* is a comparatively large mass of irregular shape and large cavity, occupying a good part of the space in the prodissoconch. In 1 mm. spat (Plate V, fig. 33) there may be considered to be three prominent extensions; one forwards below the œsophagus, another postero-dorsal behind the entrance of the œsophagus, and a third, beginning as a compressed ventral extension of the first, slants downwards and backwards towards the great adductor muscle, becoming broad, deep, regular and thick-walled. This, I am satisfied, is the portion that secretes the crystalline style, and originates postero-dorsally in the left umbo of the larva, but becomes moved to its present position during the rotation of the viscera, and presents the appearance, in the inside, of a regular, dense growth of cilia. Just in front of the insertion of the œsophagus but on each side of it, i.e. dorsolaterally, spring the stalks of the *liver*—one on the left and two on the right. These branch into numerous follicles, lying on both sides of and above the stomach, and projecting far forwards to the region of the mouth. On the ventral aspect of the stomach, in the same region, springs the *intestine*, on the right, in the crease between the compressed antero-ventral extension to the left and the main central body of the stomach above (Plate VII, fig. 6). From this the intestine passes backwards on the right, then forwards behind the rounded postero-dorsal extension, forwards and down the left side, where, near the anterior end of the stomach, it turns backwards and then down, finally passing towards the median plane to the *anal opening* over the adductor muscle. The stomach sometimes contains diatoms and desmid-like clusters of one to four nucleated cells.

During the growth into the larger spat the chief feature of the intestinal system is the downward prolongation of the part which gives rise to the *crystalline style* below the adductor muscle.

The Nervous System of the youngest stage of the spat still retains cerebral, pedal, and visceral ganglia, but the two former are already becoming difficult to recognize, while the latter are more evident than in the larva. The cerebral and pedal ganglia disappear with the velum and foot, whose purposes they serve—first the ganglion-cells and then the nerve fibres becoming reduced. The visceral ganglia on the contrary persist and become conspicuous from their size, symmetry, and position in front of the great adductor muscle (Plate V, fig. 33). They preserve a distinctly paired structure (Plate VI, fig. 15; Plate VII, figs. 6, 7) and have a central nerve mass surrounded by a layer of more deeply staining ganglion-cells. The limitation of the foot to a brief transitory existence during the free life of the oyster will explain the atrophy of the pedal ganglia. Fixation and consequent loss of activity, together with a shifting of responsibility to the gills, and the return to a degree of radial symmetry, have dispensed with the need for cephalic ganglia, and thrown everything within the range of the visceral ganglia. Two large nerves can be traced forwards, in 1 mm. spat, from the ganglia, one on each side of the descending lobe of the stomach, for fully two-thirds the distance towards the mouth.

Cephalic ganglia have been mentioned (and even figured) for the adult oyster by Ryder, Hyatt, Grave, and others, but, despite careful search through sections of different sizes of spat as well as dissections of large spat and adults, I have never been able to find them, and I fear they have been imagined by analogy with other genera in which they are easily found (Mya, Mactra, Venus, Mytilus, Anodonta, Cyclas, &c.)

Sense-organs such as eye-spots and otocysts, useful during the active life of the larva, disappear rapidly upon the assumption of the quiescent, involuntary existence of the spat. High epithelium occurs at the margin of the mantle behind the adductor muscle, in early spat stages.

A Heart having a thin wall and containing large, deeply staining, nucleated blood-cells, is situated in front of the posterior adductor muscle and visceral ganglia. In the recently attached spat it occupies the space between these and the stomach in front, and with the two lobes of the liver on the sides (Plate VI, fig. 15). In 1 mm. spat, where the adductor muscle has moved downwards and the stomach become more developed and rotated backwards, the heart lies rather above the adductor muscle and below the rectum.

Nephridia (or what I take for them) are to be found in spat of ·79 mm. and larger (Plate VII, fig. 6), as two tubes in the angles close against the adductor muscle, and running forwards on each side of the visceral ganglia. They are relatively large, hollow tubes, composed of pale, nucleated, epithelial cells. They occur in all sizes of spat, but do not retain the simplicity of the younger stages, being represented in the larger ones by several tubes side by side or branching, some of which extend far forwards to the region of the genital organs and suggest that they may later serve as genital duct. Some of them again extend far backwards

underneath the adductor muscle, where one on each side can be traced to an opening in the supra-branchial chamber (Plate VII, fig. 18).

Reproductive Organs become conspicuous in spat of 32 mm. (Plate VII, fig. 20), appearing first in sections that fall between the posterior tips of the palps and the anterior tips of the gills, and occur nearly as far back as the end of the descending loop of the intestine below the adductor muscle. In the most anterior of these sections the follicles are confined to small areas in the angles of the body, each side from the palps and close under the ectoderm of the surface. In going backwards the areas extend upwards until they form a deeply staining band completely surrounding the liver with its enclosed stomach, and in front of the heart there is a tranverse band separating the part which follows the rectum for a short distance from that which follows the descending loop of the intestine. The follicles present the appearance of portions of coiled tubes distended with innumerable spermatozoa, having a fine, parallel, fibrous arrangement in which, under high powers, the heads are recognizable as dots. The longest of the already mentioned nephridial tubes can be pursued far forwards on each side, in the extreme angles, outside of and below the the lateral areas referred to, and very close to, but not touching, the testis follicles.

In a 21 mm. spat the beginnings of follicles can be recognized in the median portion of the above defined region (Plate VII, fig. 19), although there is not a sufficient histological specialization to determine what they are going to be without comparison with sections of an older individual. Judging from these, it is pretty safe to assume that males become sexually mature at about 1 inch (=25 mm.) in length.

Part II

ENVIRONMENT AND CULTURE

PART II

Environment and Culture

I

RESUME OF THE STAGES OF DEVELOPMENT

Periods of Practical Importance.—Having described the origin from the egg and the development up to a size approaching maturity, we are now in position to cast a retrospective glance over the different stages and events and to pick out the especial forms, periods, or conditions which afford opportunities for turning the rapid reproductive and growing powers of the oyster to advantage in furnishing occupation and gain to mankind.

The most important events or processes in the developmental life of the oyster that afford possible usefulness to man are three: spawning, swarming and spatting.

Spawning is the natural extrusion of the spawn or eggs from the mother oyster into the sea-water about her. The time at which this occurs has been variously stated by different observers, most of whom have allowed a broad latitude to cover differences of place, season, variety, etc. It is also certain that the actual process, on account of the position of oyster beds below water, has been seldom if ever observed. The data for its calculation have been mostly obtained by examining the genital organs of oysters, either from the surface to observe the plumpness, colour, etc., or microscopically to note the size, shape, freedom, and structure of the eggs. This presupposes a certain expert knowledge and ability, which few people possess, and which can only be acquired by considerable experience and good judgment. It is an easy matter for a man who has studied other animals to make a mistake on the oytser. It is advisable that he should examine a large number from different beds and at different times before, near to, and after spawning as a preparation. To make sure that eggs are ripe it may be necessary to fertilize them and observe that they can develop. It will usually be sufficient, however, to observe that they flow easily from the genital opening when a slight pressure is applied. When the determination of the time of spawning is important it will be best to examine it for the place and season concerned, and to extend the examination to a large number of individuals taken from different parts of the area. A few specimens from a convenient shallow-water bed is not a safe indication of the condition of the masses.

On account of great differences between European and American oysters it is not safe to judge from analogies. The English or common

European oyster retains the eggs within the shell and between the gills for some time after they are extruded from the ovary through the oviduct, during which time they develop into straight-hinge shelled stages. The time at which these pass out into the sea does not correspond with the time of spawning of the common American or Canadian oyster. It is the time when the eggs of the European oyster pass from the ovary into the mantle-cavity that corresponds with spawning in the American oyster, and this is even more difficult and less likely to have ever been directly observed.

Sprat (1669) wrote, "In the month of May the oysters cast their spawn."

Brach (1690) thought that oysters produce spawn towards the end of spring, during the entire summer, and in the beginning of autumn.

Davaine (1852) specifies from the beginning of June to the end of September.

Huxley (1883): "During the summer and autumn months, from as early as May to as late as, or even later than, September."

Except for local differences of temperature, food, enemies, and the like, the accrued knowledge in the United States on this and other questions relating to the oyster, is of great value to Canada.

Winslow (1878), writing of Tangier and Pocomoke sounds and Chesapeake bay, remarked, "The spawning season was said to be from May until August inclusive, though most of the spawning was done in June and July."

Brooks (1880): "Oysters in from one to six feet of water in the vicinity of Crisfield, probably spawn between the middle and end of May, but oysters with ripe eggs were found in water from five to six fathoms deep from the first to the thirtieth of July, although most of them spawn late in June."

Ryder (1882-3): "In the region of the Chesapeake the most important spawning period seems to extend over the months of June and July, but considerable ripe spawn may be found even much earlier and later than this."

Nelson (1900): "Late in June and early in July this spawn is 'ripe' and is thrown out of the oysters, sometimes so abundantly as to make the water look as if milk had been poured into it." Also (1906): "It is true that eggs of some sort were present in oysters from May to September, but we have good reason to believe that the present season's supply of natural oyster seed was all produced during the last two weeks of June, if, indeed it was not still shorter.......... By the end of June the large naturals at Barnegat had completed their spawning. The young oysters were on the point of beginning to fill up with spawn a second time. This spawn, which was thrown out during July, does not seem to have played any appreciable role in producing spat." Again (1909): "Hence it is that oysters taken from the warmer southern waters and planted in the colder northern waters will fail to propagate, although well filled with spawn, and that northern oysters taken into more southern regions will spawn earlier than the natives."

In Canada, during the long winter and cold spring, the reproductive cells in the ovaries of oysters make slow progress. But with the arrival of the warm weather of May and June, and the abundance of microscopic food organisms that accompany it, the genital elements rapidly come to maturity. Late season, shaded localities, deep water, cold currents, individuality of the oyster, etc., may cause delay here and there, but the long period of cold, followed by the relatively short spell of very warm weather, tends to restrict spawning to a briefer term and to bring about a degree of regularity or periodicity.

It would require several years of observation and a careful systematic examination of a very great number of specimens from different localities

to determine the period with certainty. I believe that, while it may fluctuate to some extent according to season and locality, it will be found for the great mass of oysters to fall about the end of June and first half of July.

The temperature of water in the region of oyster beds along our coast, at the beginning of spawning, approximates to 20° C. (= 68° F.). In 1909 the surface water above the government reserve beds at Shediac, N.B., reached 17·5° C. on July 7, and an artificial fertilization experiment succeeding in developing numerous oyster eggs to the free-swimming larva stage. On August 7 the highest temperature, 23° C., was noted (at Caraquet), and on September 2 the temperature, 18° C. was already beginning to lower (at Malpeque). This was an unusually late and cool season and illustrates the dependence of spawning upon temperature, for the first young shelled stages of living oyster larvæ were observed in the plankton collections on July 22 (at Cocagne).

The number of egg-producing oysters is of course only a fraction of the whole number of oysters in a bed. There are as many males as females. Immature oysters do not spawn.

The number of eggs spawned by a single oyster of average size was estimated by Brooks (1880) to be about 9,000,000, and for a very large oyster about 60,000,000. In a later work (1905) he gives 16,000,000 as the average. Prince (1895) mentions 50,000,000 to 100,000,000. Nelson (1900) gives 30,000,000. The method of estimation consists in measuring the cubic contents of the ovary, or of the mass of ova extracted, and, after making allowance for surrounding and intervening tissue, calculating the number of times the remaining volume would contain that of a single egg. The actual number is of less real value than the fact that it is, at all events, very large.

On an undisturbed oyster bed of some years standing, the chances are that the actual number of oysters from year to year does not change to a very great extent. In such a case the collossal number of eggs spawned serves solely to make good the loss through death from natural causes, and illustrates the lavish method of nature in preserving the average number of individuals.

The fate of most eggs is in some way to meet with destruction, the manner of which will depend upon their chance circumstances. They may fail to be fertilized. At one place they may fall in masses so great that the under ones are smothered; at another place they may sink into mud and meet with a similar fate. Here falling sediment or drifting sand may encompass them; there they may be eagerly devoured by some animal. Currents may drift them out to sea where they are lost, or throw them up on the beach where they are dried. Those that escape such accidents uninjured develop into larvæ.

The length of the period during which spawned eggs remain quiescent or are moved only by forces outside themselves is about five hours.

Spawning may be turned to advantage by man, either in furnishing him with eggs for artificial propagation or in giving the time from which to make calculations for other processes, such as putting out of cultch.

Swarming (swimming) is the name I give to the second important event in the life of the oyster, affording practical information to man. It represents the free-swimming period—the period of the larva—and begins about five hours after the eggs are spawned.

The manner of observing the swarming does not depend upon handling adult oysters as spawning does. Neither does it depend upon watching the swarmers or larvæ in their natural habitat in the sea; that would be as difficult as the actual observation of natural spawning. It depends upon a method of straining sea-water and in this way collecting the swarming microscopic larvæ. A plankton* net is towed behind a boat through the water above oyster beds and the collected larvæ are kept in glass vessels full of sea-water and examined with a microscope.

This is the most recent and most productive of practical methods. It can be conveniently and repeatedly employed . It allows great quantities of water to strain through the net and retains great numbers of larvæ. It collects many ages and sizes extending over the longest and most formative period. It exhibits actual conditions. It can be applied at the right time.

The method first passed beyond its incipient curiosity stage in 1904 when I made it the basis of my plans for following up that portion of the life of the oyster which had remained unknown and brought it into systematic daily use as a necessary part of my programme. The value of the method was proved by the results.

An examination of Nelson's reports shows that he had used filter paper in 1903, but did not make much use of it until 1906, when he wrote: "In order to ascertain whether or not oyster fry are present in the water it is necessary to filter it through a fine filter, which is a slow process." It takes an hour or longer to filter a pailful of water. The larvæ cling to the paper or are washed under its folds so that it has to be opened out and rinsed. The sediment has to be examined with a microscope. Nelson employed this method a great deal in his later work. It gives the proportion in number of larvæ to the volume of water filtered. But when larvæ are scarce such small quantities of water might not yield any and thus lead to wrong results, especially if used to determine the time of the first occurrence of larvæ in an oyster region. Some of the larvæ may be easily overlooked, and in small catches this would greatly modify the proportion. In 1907 the temperature on June 18 was 70° F. and the first undoubted larvæ were obtained on the 25th or 26th. On July 5th, a half

* See footnote to page 31.

pailful of water showed 40 larvæ. On the 8th a pailful yielded 63. On the 10th a pailful gave 24, etc. These proportions appear to me to be high, but I have no doubt that the places from which the water was taken (near Barnegat and Tuckerton, New Jersey) are in a very rich oyster region.

The earliest in the season at which I have obtained oyster larvæ from the water was June 26, 1905, at Malpeque. They were 14, 15, and 16 units in length and not plentiful, although the larvæ of mussels and clams were. On July 11, 1904, oyster larvæ were plentiful at the same place and varied from 12 to 20 in length. In 1909 I planned extensive observations, and in order not to miss anything spread them over a large number of oyster areas down the east coast of New Brunswick and around Prince Edward Island. Judging the time from my experience of 1905, I began taking plankton on June 25th at Caraquet and found that I was well ahead of the season, as there were only a very few mussel and clam larvæ in the water, and these can always be counted on as first to put in an appearance. The season proved to be cold and backward and the first oyster larvæ appeared at Cocagne on July 22nd. They were small, varying from 10 to 14 in length, and few, and were mixed with the larvæ of mussels, quahaugs, scallops, and one or two other bivalves.

The number of oyster larvæ, as viewed for a single season, begins with a minimum, rises to a maximum, which is held for a period, and then falls to a minimum again. The same is true for each bay considered as a whole, although one bay may be a few days in advance of another. It is also true for each oyster locality in a bay, even though one of these precedes another in time. In each locality, such as the region about an oyster bed, the first larvæ to appear are small and pretty uniform in size. Succeeding catches will soon show a mixture of larger and smaller individuals because the first will have grown while the fresh ones are coming on. Daily examination of plankton collections will keep the observer informed as to the progress of the largest larvæ until they reach their full size (55 units) and at the same time the relative proportions in numbers of these older larvæ to the younger swarms with which they are associated. He can also estimate approximately the age of the oldest ones, the length of time before those of any particular size will be of the same age, and at what time there will be the greatest number of full-grown larvæ in the water. As this time approaches he will be in a position to judge if there are better prospects arising. In a bay of some size there may be several such oyster areas and then the conditions become more complicated. The larvæ from one may be carried over into another by the ebb and flow of the tide. This may in places be a simple oscillation which carries the water back and forwards without mixing it to any great extent; but in some cases there result tidal currents which draw water from different directions, mix it, and carry it to a considerable distance, never returning it to the same place.

The entrance to the bay, whether wide or narrow, the deep channels and the broad flats, the presence or absence of islands, the water brought down by rivers, and all such conditions, have to be taken into consideration, as well as the situation of the oyster beds, in the interpretation of the plankton and in the selection of places from which to collect it. A person uninformed in these matters might be confining his attention to a region where there are no oyster larvæ at a time when they are plentiful elsewhere. The larvæ do not by their own activity wander far from their birthplace. There is a falling off in quantity depending upon the distance from the centre of origin. If centres are not far apart the dispersing larvæ may intermingle, if the centres are distant there may be intervening masses of water devoid of larvæ. Plankton taken off one side of a small island may contain oyster larvæ while that from the opposite side does not. On the way from one oyster bay to another the water does not ordinarily contain oyster larvæ. If it does, it is because of tide currents. In going outwards into the gulf of St. Lawrence or into Northumberland strait from an oyster region the larvæ soon dwindle out. Over a deep-water bed the numbers diminish from lower to higher strata. Storms, breakers, tide currents generally cause larvæ to sink, but if not too violent the larvæ may become habituated to them. In shallow water the disturbance may reach to the bottom and whirl up larvæ in the same way that it does ooze, sand, mud, and weeds.

In estimating the number of larvæ in an area at different periods, or in calculating the productiveness of different areas, it is usually sufficient to make a relative comparison. This may be done by dragging a plankton net through the water under the same conditions and for the same distance in the different cases and measuring the volume of bivalves collected; then making microscopic preparations from the under settlings by spreading out a uniform thin layer and counting the number of oyster larvæ under a definite size of cover-slip or in a certain field of view. The more nearly the examination can be made to cover the whole area and the greater the number of tests, the more accurate will be the conclusion. At the beginning of the season oyster larvæ will be few and small, although mussel and clam larvæ may be plentiful and of various sizes. At this time counting is difficult on account of the small size and similarity of different species, but an estimation of numbers is not so likely to be required as the recognition of their presence. On June 26, 1905, plankton taken up Shipyard basin (Malpeque) showed few oyster larvæ; that across Keir bay (out from the March water) contained many; that off Ram island few. Mussels were few, clams numerous. On July 11, 1904, between Ram and Curtain islands there were many oyster larvæ but few mussels and clams. On the 14th over the Curtain Island beds there were many oysters, few mussels, more clams, and an odd quahaug or scallop. On the 27th I took the best catch for the season. Most of the larvæ were now grown to their

characteristic shape and were easily counted. Prepared in the way mentioned there would be about 25 oyster larvæ under a ¾ inch cover-slip and about seven times this number of other bivalve larvæ. The numbers kept up for a few days into August and then began to fall off, at first slowly, but from the 20th rapidly, and after the first of September scarcely an oyster larva could be found. In 1909 the season was cold and backward. Small larvæ first occurred on July 22nd (at Cocagne). The numbers increased beyond previous observations. At Bay du Vin on August 5th, I counted 83 oyster larvæ under a ¾ inch cover-slip. At Malpeque on August 26th I counted 35 in the field of view (Oc. 3, obj. 2). On August 30th I counted 150 under one cover-slip. I have preserved plankton for September 3rd that shows an average of a dozen oyster larvæ in each field of view. I did not wait to see the decline of the oyster season that year, but I calculated from the appearance of the first larvæ that the season was about three weeks late.

The rate of growth of oyster larvæ cannot be determined by keeping them confined in small glass vessels where they may be easily found and observed. The temperature and aëration conditions are unnatural and the food supply is shut off. Close observation of plankton-catches at the beginning of the season will show that the largest larvæ of one day's collection will be larger than the largest of a previous day. At Malpeque, July 11, 1904, the oyster larvæ taken could be arranged according to length from 12 to 20 (·083 mm. to ·138 mm.) On the 14th lengths of 21 to 26 (·145 mm. to ·179 mm.) could be added. On the 27th from 30 to 46 (·207 mm. to ·317 mm.). On August 3rd, from 47 to 52 (·324 mm. to ·358 mm.) This would seem to show that it requires at least three weeks to grow from the smallest shell-covered stages to the full-grown larvæ. In 1909 the first oyster larvæ of July 22nd at Cocagne measured 10 to 14, those of July 26th, 11 to 27, those of August 2nd, 29 to 38. On August 4th, at Bay du Vin, I first observed full-grown larvæ of 54 units (about 1/66 inch) length among numerous others ranging from 29 to 50. From this it would appear that the larvæ grew from the smallest to the largest shelled stages in about two weeks. There is a possibility that Bay du Vin larvæ were slightly in advance of those of Cocagne. I had taken plankton there on July 13th, nine days before the first larvæ occurred at Cocagne, and there were no oyster larvæ at that time, so that any advance was less than nine days. Lateness of spawning, a continuous and very warm spell after the long cold spring, abundant food or other causes, may have hastened development. But, if so, these causes did not shorten the season, for there were swarms of larvæ in the water at Malpeque on September 3rd. I prefer to think that the season of 1909 was not so near the average as that of 1904, and that three weeks is nearer than two weeks for the average normal growth of the larvæ through the shelled stages.

The length of the period of an oyster's free-swimming life may be considered to be between three weeks and a month. The period of five hours from fertilization to the beginning of swimming locomotion is so short as to scarcely need consideration in this connection. The period of thirty-two hours from fertilization to the first beginnings of the shell is likewise a comparatively short time. The period from fertilization to the earliest plankton stages, i.e., to the larva (such as raised by Brooks) with a straight-hinge shell sufficient to enclose the soft parts, is as closely as we can calculate, perhaps six days. This with the three weeks of growth from the youngest to the oldest plankton stages, makes approximately a month for the whole period.

Swarming can be made of great advantage to man in that, by repeatedly taking and examining plankton, he may learn the time of the first appearence of oyster larvæ in the water and keep informed as to their numbers and growth, and thereby be able to judge the best time for putting out cultch.

Spatting is the natural and normal fixation of full-grown oyster larvæ on to shells, rocks or other solid objects in the sea-water of oyster areas. The actual process, we may feel assured, has never been observed, but spat have been discovered so close after being fixed that their fixation was the only recognizable and essential difference between them and the oldest free-swimming larvæ. The first apparent difference in structure to arise is the deposit of a rim of new shell, the spat shell, which soon grows to such an extent as to make the spat easily visible and recognizable as a minute oyster. Older and larger spat have long been known by men who have had to do with oysters. They seem generally to make their appearance so suddenly that it is customary among fishermen to speak of a "fall of spat."

The time of the year at which spatting takes place has not received much attention from those who have studied the development of the oyster. Perhaps this is due to the failure to separate spatting from spawning. So long as it was believed that fixation takes place in a brief time after the eggs are spawned there was no particular advantage in considering the two periods separately.

Sprat (1690) wrote: "In the month of May the oysters cast their Spawn (which the Dredgers call their Spat)."

Winslow (1882): "The oyster embryo is predisposed at least to fix itself very soon after the process of segmentation is completed."

Rice (1885): "The attachment takes place in about two days from the time of fertilization."

Jackson (1888) .... "when oysters were setting most abundantly in July and early August."

Nelson (1901): "The fry, after about five days, develop a two-valved shell, and then they seek a place to settle down on."

The first spat of the season 1904 that I observed was taken on the 16th August. That this date is sufficiently near the mark is proved by

the fact that I was looking for spat every day in the same manner, and that up to that date I had found none, but afterwards I found many both on glass strips and on shells, and they were all extremely small. In 1909 the first spat I captured was on the 19th August, taken at the same place and in the same manner.

The number of spat is small at first, rising to a maximum, and then falling. At first it is necessary to examine many shells to find a single minute spat. In a week or two it may be possible to find one, two, or three on almost every shell. I have never seen anything like such numbers as Ryder, Rice, Brooks, Nelson, Grave and others have described and figured.

Ryder (1883): "As many as 25 young oysters might have been counted on a surface of one square inch," (on wooden buoys taken up early in July near Woods Holl), and again "more than 100 oysters on a single shell."

Rice (1885) figured the inside of an old oyster valve with 165 spat attached.

Brooks (1905) figured an oyster shell bearing 150 spat.

The rate of growth of a young spat has been observed by Jackson (1890, Plate XXIV, fig. 3). He caught a spat on glass, so recently attached that there was no additional growth to the larval shell, and kept it alive in a beaker of sea-water for four days. In three days it almost doubled its height.

An experiment of my own at Malpeque in 1904, in which the spat comes next in size to that of Jackson, shows one half the rate of growth. This spat was procured on the afternoon of August 31st at Ram island, about six miles from the station, and measured at 5 p.m. ·861 x ·953 mm. in height and length. It was kept under the arch of the wharf until the afternoon of September 1st and measured again, but it showed no increase in size. It was then taken to Ram island and placed under its original conditions, but in a crock, and at 4 p.m. September 7th, it measured 1·276 x 1·260 mm. It was kept in running sea-water until 5 p.m. of the 8th, and then put under the arch of the wharf until the morning of the 9th, when it was again taken to Ram island. It did not grow either in the running water or under the arch of the wharf, where there is at times considerable tidal current. On the forenoon of the 16th it was again brought in and measured 1·753 x 1·661 mm. It would appear that the spat did not become immediately accommodated to new conditions after being disturbed. As the measuring was made at intervals of six and seven days it is impossible to say how much of the time was taken up in getting accommodated and how much in actual growth. If we start with the size of the largest larval shell, ·369 mm., and, taking Jackson's results, add one-third for each day's growth, the heights would be ·492 (one day spat), ·615 (two day), ·738 (three day), ·861 (which was the height of my spat at the beginning), ·984, 1·107, 1·230 (approximately the height of my spat after six days growth), 1·353, 1·476, 1·599, 1·722 (approximately the

height of my spat after seven days additional growth). It will be seen that my spat only added in six and seven days what Jackson's would have done in three and four days.

I planned an experiment on growth through the winter by putting out closed strong wire baskets containing oyster shells upon which were marked specimens of minute dark spat. But these could not be found next spring and I supposed that they had been tampered with—perhaps by the early lobster fishing. Examination of shells off Ram Island point at the beginning of June, 1905, showed some dark spat still there that had apparently not grown a bit, or changed in colour during the winter. Many had died and lost the upper valve or both valves, sometimes leaving a patch or rim showing where a spat had been. The largest dark spat collected the previous autumn measured 6 mm., and the largest now were 8 mm. in height. They retained their dark metallic lustre with radiating ridges or lines and very thin edges—the whole spat being thin and fitting so solidly against the supporting shell as to require some force with a knife-blade to separate it. In some of the larger was to be seen a tendency to turn white, in that the dark rays were irregularly separated by reversed lighter radiations. It would seem that on our coast oysters do not ordinarily grow beyond these dark spat in size during the first season; that the spat growth takes place during the remaining short period of warm weather after the middle of August; that no growth takes place during the winter, except perhaps a slight thickening of the shell.

Winslow's experiments in Chesapeake bay showed spat caught on tiles grown to $\frac{3}{4}$ inch in 3 months.

Ryder says that after fixation the growth of spat is very rapid—in a week or ten days to $\frac{1}{4}$ inch across, 20 days $\frac{7}{16}$ inch, 44 days $\frac{13}{16}$ inch, 48 days 1 inch, 79 days $1\frac{3}{4}$ inches, 82 days 2 inches.

It is possible to pick out all sizes between the little dark spat I have mentioned and mature oysters of four and five inches. It is also possible to arrange them into groups varying about a few definite sizes. The larger specimens have characteristic concentric ridges and furrows, representing periods of growth and rest that correspond in sizes with the smaller ones. The most regular and typical of these must have reference to the annual growth. I think it likely that the first deep furrow, somewhere about 1 inch from the umbo, marks the close of the first full year's growth—i.e., a full year from the cessation of growth of the $\frac{1}{4}$ inch (6 mm.) dark spat. The next complete deep furrow, somewhere about $1\frac{1}{2}$ to $1\frac{3}{4}$ inches from the umbo, may indicate the size at the end of two full years. Another furrow, about $2\frac{1}{2}$ inches or a little more from the apex, three years. There are secondary furrows, irregularities and perhaps exceptions, and the measurements vary according as the oyster is of the long or the short variety. I have not sufficiently examined this feature and have had no

opportunity to subject it to a practical test, but it may be worth following up with a view to becoming able to judge of the age of oysters.

If the above suppositions are correct, then male oysters become sexually mature at a time when they exhibit only one complete year's growth (1 inch), but when they are beginning their second year's growth, and are really in the third summer of their existence. During the first autumn they grow to $\frac{1}{4}$ inch or thereabouts and then rest; with the arrival of warm weather the next summer they begin and carry on a vigorous growth until again arrested by cold weather and scarcity of food; in the spring and early summer of the following season they set about developing the reproductive organs and begin a new period of growth.

In a retrospect of the processes of spawning, swarming, and spatting, the time of the year mentioned for each is of course the beginning of the process. If it were possible to observe, and to confine our attention to a single egg, naturally spawned, and, under normal conditions, watch its development, the matter would be simplified in that the processes would be separated and follow in the order named. If it were possible to observe a single oyster, taking its natural course, and to watch the development of its spawn, under normal conditions, there would be somewhat greater complexity; even if the eggs were all extruded* at once some of them would soon begin to develop faster than others, with the result that the succeeding processes would to some extent overlap. On an oyster bank there may be millions of oysters; they spawn millions of millions of eggs—each oyster when its eggs are ripened or it feels the impulse; the first oysters spawn considerably in advance of the last ones. In an oyster area of different beds under widely divergent physical conditions, the first oysters spawn the whole length of the spawning period before the last ones; spawning, swarming, and spatting may overlap, to the extent that the first brood may reach the spat stage before the last eggs are spawned. Matters become so complicated that the observer may have any or all stages between and including the extremes presented to him at once. He then loses sight of individuals and thinks of aggregates and processes.

Viewed as a whole, each of the processes of spawning, swarming, and spatting begins with a minimum number, rises to a maximum, which is held for a time, and then commences to decline. Spawning is first com-

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*With regard to the extrusion I may mention a single case. I was busy in the cabin doorway of the "Ostrea," opening oysters to procure ripe eggs and sperms. At times the sun shone upon a little heap of oysters on the deck in front of me. I suddenly heard a squirting noise and looked to find one of the upper oysters nearly covered with a discharge of eggs. The occurrence does not prove however, that this is the normal method of extrusion, since the oyster may have been irritated by the heat or by a jar, and suddenly snapped its valves towards each other, pressing on its body and forcibly squeezing what eggs were already ripe from the oviduct. The normal discharge may be more of the nature of a gradual flow of those eggs that become ripe and free, backed up by the pressure of growth behind or by the ordinary movements of the body.

That eggs of the same brood do not develop uniformly can be seen in a beaker containing the products of any fertilization experiment.

pleted, then swarming, and finally spatting. After that there are no eggs or larvæ left in the water, but there are the successful spat. Spatting depends upon swarming and this upon spawning. Given the time of spawning and the period of development, the time of spatting may be calculated. Given swarmers (larvæ) in any particular stage, size or age, and the succeeding period of development and the time of spatting may be calculated. *Spatting is the all important event. The value of the oyster harvest does not depend upon the number of eggs spawned, nor upon the number of larvæ in the water, but upon the number of successful spat.* It is impossibe to observe spatting directly, but it is possible, by close observation of shells and other objects in the water to find some of the first deposited minute spat, to approximate to the time when it begins. The information however, may come too late for practical purposes. Hence the necessity for relying upon earlier data. Spawning, like spatting, cannot be observed directly, but, indirectly, it can be approximately fixed. The method is laborious, the information limited and easily mistaken, and the time so far antedates spatting as to leave room for accidents that can not be foreseen. Swarming follows spawning and precedes spatting, so that information gained from spawning can be followed up and subjected to verification throughout the period of swarming to the very point when it is to be turned to account in the capture of spat.

After making use of all the methods, the information acquired holds good only for the season to which the observations belong. Nevertheless the events of one season point in a particular way to what may be expected in another season; to be forewarned is to be forearmed; and it is important to limit these events, as far as possible, to particular dates and periods of time. To do this with any degree of satisfaction, it would be necessary to carry on a series of observations of these points through a number of years. Hitherto my own observations have been confined to two pretty fully utilized seasons and a small portion of each of two other seasons. In the first season, that of 1904, the subject was not sufficiently matured to permit of being made use of to the best advantage. In 1905 my observations were confined to the month of June. In the third season, that of 1909, the necessity of moving from one place to another in order to determine other points was a disadvantage so far as the present subject is concerned. In 1911 my observations were on the Pacific coast.

Date and Duration of Each Period.—Putting together what was relative to the subject on these different occasions it would appear that:

Spawning is pretty likely to begin in the first week of July, rise through the second week to its maximum in the third week, and then decline in the fourth week. Continuous warm weather may bring it on in the last week of June, persistent cold weather may hold it off until the third week of July.

Swarming (swimming or larval stage) begins within a few days after spawning, keeping parallel with and exhibiting like fluctuations.

Spawn of the first week of July is in the straight-hinge stage of the larva in the second week, entering the umbo stage in the third week, and approaching full size in the fourth week. The abundant spawn of the second week of July accounts for the numerous grown larvæ of the second week of August. The decline in spawning towards the end of July is responsible for the diminution in numbers of larvæ at the end of August.

Spatting (fixation of the larvæ to solid objects) begins about a month after spawning, keeping parallel with and exhibiting fluctuations similar to both spawning and swarming. The first minute spats found about the middle of August are likely to be already several days old and to have come from eggs spawned in the second week of July that became developed into full-grown larvæ in the second week of August. This will allow the really first spat, to go unobserved on account of being few and scattered and leave the last two weeks of August for the completion of development and spatting of the late larvæ, which in a backward season may lag into September. Judging from a comparison of 1904 and 1909, when the reproductive processes are kept back by cold weather for a time they move all the more rapidly when fine weather does arrive. In 1904, on July 11, larvæ measured 12 to 20 (·083 mm. to ·138 mm.) and the first spat was observed on August 16. In 1909, on July 22, larvæ measured 10 to 14 (·069 mm. to ·096 mm.) and the first spat was observed on August 19.

II

ENVIRONMENT OF THE OYSTER

IT is understood that for eggs to be produced and developed through the spawning, swarming, and spatting periods there must exist certain pre-requisites in the biological and physical conditions of the environment.

The Biological Conditions for the oyster are not markedly different from those of any other highly organized living marine animal, and consequently do not afford any special clue of a practical value to man. Oyster eggs must originate in oysters that have themselves found suitable or at least tolerable conditions. The food stored in the eggs is a hereditary gift from the parents. The external conditions that are not immediately destructive to oyster eggs are to some extent favourable to the production of minute organisms that may serve as food for the larva, spat, and adult oyster, thus supplying a most important biological necessity. Competition for food and place, defence against enemies, and other physiological or bionomic activities on the part of the oyster are so nearly identical with those of other animals that it would not help in our present purpose to consider them in detail. The functions of cells, tissues, organs, individuals, or whole collections of oysters on an oyster bed or in an oyster bay, when analyzed, bear a relation to the physical environment with which we can deal to greater advantage.

The Physical Conditions of natural oyster-producing, as compared with non-oyster-producing, areas will determine the prime essentials, not only for the life of the oyster, but for the successful production of eggs, larvæ, and spat. Along our coast the oyster lives and breeds in comparatively shallow bays, coves, and estuaries of rivers that are sheltered from the deep, cold, often stormy waters of the gulf and ocean by islands or projecting long sand-bars; that have areas of less than three fathoms depth, a tidal fluctuation of only 3 to 5 feet, and some admixture of river water; with rather hard bottom of rock, stones, gravel, clay or sand, often over-laid with a dark-coloured, light, loose, fluffy ooze of organic origin, but no deep, heavy, sticky mud or shifting sand. The salinity generally lies between 1·012 and 1·020 (distilled water being 1·000) but varies a few degrees with the ebb and flow of the tide and with the amount of river water. In the early part of July the temperature of the water approximates to 20° C. (= 68° F.) and, owing to the small exchange of tidal water and the great amount of heated sand, there is no great and sudden variation. Such

physical conditions are also favourable to the presence and muliplication of numerous diatoms and other minute food-supplying organisms.

A tidal rise of 3 or 4 feet, especially when flowing among islands or over sand-bars or extensive flats, does not bring such a deep and sudden change of cold water as to dangerously lower the temperature beyond the power of accommodation of the oysters. In many cases the water brought up by the tide is to a large extent the same as was carried out by the previous tide, and has consequently not been cooled by extensive mixing with ocean water. It is warmed by the sun and by contact with the air and with the extensive sand-beaches of the shore and of islands, sand-bars and sand-flats. The oscillation of the tides back and forward mixes colder and warmer water and saltier and fresher water, and preserves a greater uniformity, effects aëration, distributes food organisms, and carries eggs and larvæ to new areas.

The depth of water in which the great masses of our oysters are found varies from from one to three fathoms. At places, there are considerable numbers exposed between the tide-marks, while at other places there are oysters so deep as to be unattainable by the tongs. Oyster beds, banks, or reefs that come to within 2 or 3 fathoms of the surface may be surrounded by much deeper water, as is the case with the Curtain Island beds, from which the depth falls off rapidly to 4 or 5 fathoms.

A river, or in case of extensive areas several streams of *fresh water* may discharge over or in proximity to the oyster beds.

The salinity may vary to a great extent without endangering the life of the oyster. At Bay du Vin it is as low as 1·012, and at Shediac as high as 1·020. At Caraquet it varies from 1·016 to 1·019, according to whether taken at low or high tide, for in the former case there is a greater proportion of river-water and in the latter of sea-water. The low salinity of Bay du Vin is due to the large amount of fresh-water brought down by the Miramichi river. At the mouth of Miramichi bay the salinity is 1·019—the same as at Malpeque, Cascumpeque, Summerside, Cocagne, and most other places bordering on the Gulf or the Strait.

Lime (*calcium carbonate*) is required by the oyster for the construction of its shell, which forms the greater part of the weight of the oyster. The amount of this existing in oyster (not to speak of other) shells is enormous, all of which, or the constituents of which, must be contained in the water. It comes from the disintegration of old shells, from rocks in the ocean and along the shores, but especially from the river-water that has drained through the land and over the rocks of river-basins. It constitutes a small portion of the 12 to 20 parts in 1,000 of sea-water that we call salt, the greater portion of which consists of common salt (sodium chloride). The small amount of calcium carbonate is of great consequence to the oyster, and may be the chief factor in limiting the size to which oysters attain.

The temperature of the water where oysters abound varies with the year, the month, the physiography of the contiguous land, prevailing winds, the size, shape, and depth of the body of water, the nature of its entrance, the presence of islands, reefs, sand-bars, shoals, flats, the extent of the shore, amount of river-water, evaporation, sunshine, fog, and such-like conditions. The oyster itself can withstand considerable changes of temperature—it is the developing young that suffer. Accordingly there has arisen a periodicity in the spawning which falls in the warmest part of the season. As soon as the snow and ice have disappeared and the spring freshets subsided, the water gradually rises in temperature and becomes inhabited by increasing numbers of microscopic plants and animals. In May and June oysters, like other large animals that live on such minute plankton organisms, begin to ripen their eggs and spawn in time to give their offspring the advantage of the long spell of comparatively calm and warm water. At Shediac, on July 7th, 1909 (which it must be noted was a backward season), the water was at 17½° C. (63½° F.); at Cocagne, July 10th, 17½° C.; Richibucto, July 12th, 16¼° C. (61¼ F.); Bay du Vin, July 13th, 19° C. (66¼° F.); Buctouche, July 17th, 20° C. (68° F.); Cocagne, July 22nd, 19° C.; Summerside, July 30th, 21½° C. (70¾° F.); Shediac August 2nd, 22½° C. (72½° F.); Richibucto, August 3rd, 19°; Bay du Vin, August 5th, 20½° C. (69° F.); Caraquet, August 6th, 20° C. The temperature was sustained throughout August, but began to fall off in September.

The water of coves and of small inlets is warmer than that of large bays, and these are warmer than the gulf or the ocean. In crossing from the north-east corner of New Brunswick to the northern point of Prince Edward island on the 13th of August, 1909, the temperature of the surface water changed from 17¼° C. (63° F.) at Shippigan to 16° C. (60¾° F.) half way across and to 18½° C. (65¼° F.) at Cascumpeque. The temperature of the water upon reaching Malpeque next day was 20½° C. (69° F.), which is to be explained by the inland, land-locked position of the bay, the level character of the surrounding cleared land, the great extent of the shore, the immense amount of sand exposed to the sun at low tides, and the comparative shallowness of the water. The deeper and more open water about the wharves at Caraquet on August 6, 1909, was at 20° C. (68° F.) and the salinity 1·018, while the shallow water at the head of the bay, where the oyster beds are, showed a temperature of 23° C. (73½° F.) and a salinity of 1·016. The fresh water of streams when issuing from springs or flowing through forest land or deep ravines is cooler than the sea-water into which it empties. At Departure bay, B.C., July 28, 1911, at 2 p.m., on a hot day, with the tide just beginning to rise, the temperature of the water at the end of the floating wharf was 24° C. (75¼° F.) and salinity 1·016¾. At Cable point, about 100 yards away, where the tide from the gulf of Georgia flows into the bay, it was 19° C. (66¼° F.)

and 1·018 salinity. The water of a small creek, reduced by hot weather, emptying between these two positions in a shaded ravine, was $16\frac{1}{2}°$ C. ($61\frac{3}{4}°$ F.) During the advance of warm weather the surface water is colder than the air and deep water is colder and more saline than surface water. But this may be modified by circumstances. As the air is more mobile than the water, there may come a cold wave from a great distance and settle down over warmer surface water, which may then become colder than the water underneath and yet not sink, because of its less salinity. Sea water that has been spread out on the surface of a bay may be brought up by the tide and backed under colder river water.

A *bottom* of some degree of hardness is required for oysters to rest upon, otherwise they will sink and be smothered,. Rocks, stones, gravel, shells, submerged logs, stakes, or other natural or artificial objects serve very well, but these are generally lacking off shore, where the bottom is most likely to consist of clay, sand, mud, sediment, and ooze. This is the reason why on natural grounds there are so many places devoid of oysters. The oyster overcomes this difficulty to a large extent through the dispersal of its larvæ over wide areas; some of them may come in contact with a chance object as a stone or a shell and become attached. This serves for the fixation of many more in succeeding years, that in their turn furnish fresh places for attachment until an oyster bed is formed. Dead shells are as good as living oysters for this purpose, and if they break away from one another they are all the more likely to roll apart and extend the base. In time, a large area may be covered, the younger oysters building upon the older until an oyster-bed, oyster-reef, oyster-bank, or so-called oyster-rock of great breadth and several feet in thickness may result.

The natural position for an oyster is to be fixed with its left valve to the sub-stratum on which it rests, with the right valve uppermost. But they cannot all find places on top; the surface of an oyster bed is very irregular, with cuts, chasms, pinnacles, and ridges; and the free-swimming or creeping larva may become fixed to any surface of a projecting shell with the result that many are turned edge or end upwards. Spat that are separate from one another when young, often impinge against one another as growth proceeds. Many become abnormally lengthened, bent, twisted, or otherwise distorted in shape by crowding. Sometimes the growth of one presses upon and closes the shell of another to the extent that in time it is prohibited from feeding. Such a rough, irregular, honeycombed mass acts as a filter to the water that is moved by tides, currents, and waves, effecting a deposition of silt, ooze, weeds, and other things carried in suspension. This keeps settling into the interstices between the oysters until the lower ones are buried and only the upper have free access to the food-supplying water. Small scattered clusters occur that have originated in a similar way to the beds. Single individuals, that have outgrown the small objects to which they were attached, or that have been broken away

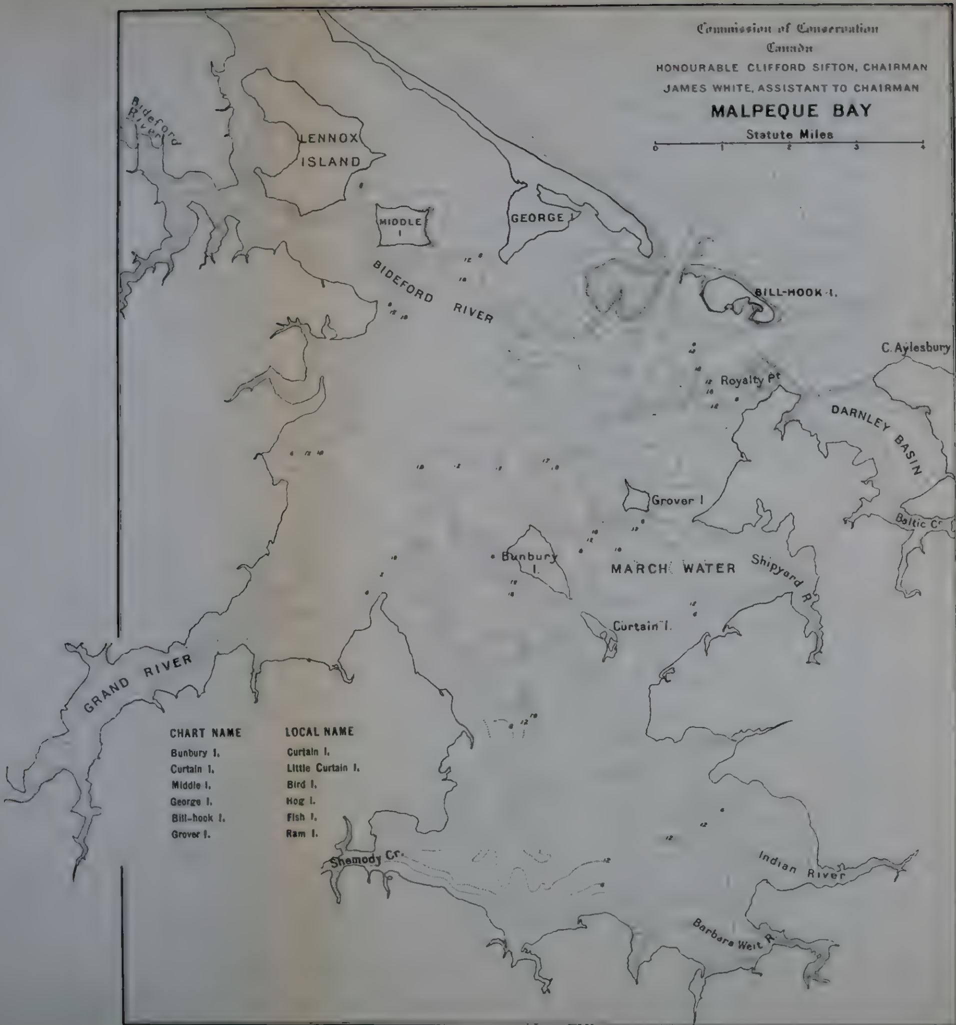
from their support and rolled about by rough seas, may be found dispersed near the shore and at long distances from oyster-beds. Under all these conditions many oysters must become separated from their support and tumble into soft mud, or fall with the flat side downwards, burying the open edge of the shell, or become covered with sediment or drifting sand. I have no doubt that the strong ciliation of the gills, palps and mantle, can do a great deal in clearing away mud, silt, and ooze, so as to permit free access of water; but the adult oyster is a very helpless animal as compared with its relatives and associates, since it possesses no foot or other organ by means of which to creep out of the mud or turn itself over. Neither can it eat its way out, although mud is often found in its intestine. As a result, vast numbers succumb to the ruthless processes of nature, their shells serving as points of fixation or sinking into and stiffening the soft bottom and thus preparing better prospects for coming generations.

The kind of rock upon which oysters may be fixed does not appear to exercise any direct limiting influence. Sandstone, granite, limestone, may be equally tenanted, and the soils derivable therefrom may be of an arenaceous, argillaceous, calcareous or other nature. But, judging from the great importance of the shell as an organ of defence against predaceous fish, as well as of fixation and support, it would seem that there may be some advantage from the proximity of limestone.

There is an observable likeness in the *situation, direction of extension, and protection* at the entrance of our best oyster-producing bays that doubtless has something to do with their fitness for this purpose. Their situation on the eastern and north-eastern coasts of New Brunswick and Prince Edward Island and to a smaller extent of Cape Breton may occasion their general eastern and western extension with eastern outlets. The bays of the southern coast of New Brunswick and Nova Scotia with a general northern and southern extension and outlet are not oyster producers, although they are farther south and nearer the great oyster areas of the United States. Bedeque and Hillsborough bays, opening on the south-western side of Prince Edward Island, can hardly be called good oyster bays, and the former is almost depleted of oysters while the best parts of the latter are so far inland as to almost count as belonging to the north-eastern coast.

Structure of Typical Oyster Bays.—Caraquet, Bay du Vin, Richibucto, Buctouche, Cocagne, Shediac, Malpeque, are typical of our oyster producing bays, and they are each guarded by a promontory, which is continued as a chain of islands, a sand-reef or sand-dunes, that act as a natural break-water and protect against the larger, deeper, colder, more restless, irresistible and stormier body of water outside.

It may be noted that Caraquet, Buctouche, Cocagne, and most of the smaller oyster systems are of a simple type—each with its river, bay, and


Commission of Conservation
Canada
HONOURABLE CLIFFORD SIFTON, CHAIRMAN
JAMES WHITE, ASSISTANT TO CHAIRMAN
MALPEQUE BAY
Statute Miles
0 1 2 3 4
Bideford River
LENNOX ISLAND
MIDDLE I
GEORGE I
BIDEFORD RIVER
BILL-HOOK I.
C. Aylesbury
Royalty Pt
DARNLEY BASIN
Grover I
Baltic Cr
Bunbury I.
MARCH WATER
Shipyard R
Curtain I.
GRAND RIVER
CHART NAME
LOCAL NAME
Bunbury I. — Curtain I.
Curtain I. — Little Curtain I.
Middle I. — Bird I.
George I. — Hog I.
Bill-hook I. — Fish I.
Grover I. — Ram I.
Shemody Cr.
Indian River
Barbara Weit R.

guard—having a circumscribed oyster area. Richmond (or Malpeque) bay is of a more complete type, consisting of several modified systems behind an extensive common guard. This is of a double nature. On the outside and extending from the entrance of Malpeque harbour in a north-westerly direction to Cascumpeque, a distance of forty-five miles, there is a series of almost continuous sand-ridges varying in height from 20 to 45 feet. Inside of this is a chain of islands: Bill-hook[1], George[2], Middle[3] and Lennox. The narrow entrance is to the east between Bill-hook island and cape Aylesbury.

The bay is irregularly quadrangular in shape, the east side being some ten miles in length, the west over sixteen, while the greatest breadth is about eight. It may be regarded as having five chief extensions: Darnley basin with Baltic creek, March water (Malpeque bay in the restricted sense) with Shipyard river on the east, the "Upper bay" with Indian, Barbara Weit and some smaller rivers on the south, and the estuaries of Grand river and Bideford river on the west. The eastern mainland between the March water and the Upper bay is almost continuous through Curtain island with Bunbury island. In a similar manner the mainland to the north of the March water is continuous at low tide with Grover island. The channel at its narrowest part, between Bill-hook Island light and Royalty point, is 8 fathoms in depth, but it soon shoals up to half as much. Opposite Grover[4] island it branches into the part which enters the March water between Grover and Bunbury[5] islands and the part which, taking a wide sweep round Bunbury island, gives off branches towards Bideford and Grand rivers and continues into the Upper bay. The deepest parts between Curtain[6] island and Bideford are about 5 fathoms, in the Upper bay about 4, and in the March water about 3. Towards the land on all sides the water becomes so shallow that one is able to wade long distances from shore. The Malpeque wharf, situated near the mouth of Shipyard river, is 1,050 feet in length.

The great masses of the oysters are towards the south and west. Deep-water beds occur along the channel to the west of Bunbury and Curtain islands. Shallow-water oysters are most abundant in the Upper bay, in Grand and Bideford rivers, about Lennox and Grover islands and in the March water.

In several respects the gulf of St. Lawrence repeats on a large scale a similar structure. The island of Newfoundland forms an enormous guard with exits at Cabot strait and the strait of Belleisle. A line from the northern point of Cape Breton curving outwards past the Magdalen islands and then inwards to cape Gaspe marks off a deep eastern and northern part from a shallow western and southern portion. The great volume of

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[1] Locally known as Fish island
[2] " " " Hog island
[3] " " " Bird island
[4] Locally known as Ram island
[5] " " " Curtain island
[6] " " " Little Curtain island

water brought down by the St. Lawrence river sweeps past Anticosti island into this deep channel and then outwards to the ocean. From Caraquet on Chaleur bay to the Bras d'Or lakes of Cape Breton, curving with the coast and enclosing Prince Edward Island, is one extensive oyster region, the great shallow Acadian gulf, whose waters are tempered by similar causes to those already defined for a single small oyster bay.

Contrast with the Bay of Fundy.—That this is the case may be judged also by comparison with the next great indentation to the south—the gulf of Maine and its extension, the bay of Fundy. The waters of Northumberland strait and of the bay of Fundy are only separated across the isthmus of Chignecto by about 17 miles of land, and yet there is a surprising difference in the aspect of the shores, the height of the tide, the temperature of the water, the nature of the bottom, and the character of the flora and fauna of the two regions. The gulf of Maine and bay of Fundy are somewhat like a funnel—having a wide open mouth and a narrowing prolongation which however does not possess a second opening. Between cape Sable and cape Cod is a wide channel of over 100 fathoms depth, which becomes curved and narrowed, but continues deep between Digby and Grand Manan. The Labrador current, descending to the outside of Newfoundland, sweeps westward between Nova Scotia and the Gulf Stream, bringing cold water to the deep channel entering the gulf of Maine, where some of it is caught by the great tide and carried up the bay of Fundy. The cold, deep water, the high tides and strong currents, the steep shores and the great amount of mud may be mentioned as the chief causes why the oyster, the quahaug, Clidiophora and Tottenia, are not found in the bay of Fundy, although they occur in the gulf of St. Lawrence to the north and again from cape Cod southward. A few oysters are to be found on the southern shore of Nova Scotia, to the east of Halifax (as at Musquodoboit) and in the south-western portion of the gulf of Maine, thus partly connecting the oyster districts of Canada with the great oyster regions of the United States.

Distribution of Atlantic Fauna.—When the first settlements were made on the New England and Acadian coasts, oysters were found to be more plentifully distributed up the shores of Massachusetts, New Hampshire, and Maine, and along a large portion of the southern Nova Scotia sea-board, including Sable island. The interesting and important researches of Ganong into the oldest historic records of this country prove that the northern distribution of the oyster has been considerably more extensive than at present. Nicolas Denys, writing in 1672, mentioned oysters at the mouth of the Grand Pabos river on the north of the bay of Chaleur, and in 1664 there were said to be numbers of good oysters in the neighborhood of Percé island near the entrance to Gaspe bay. That this was possible is supported by those remnants of former periods exposed in

Indian shell heaps and in Pleistocene fossils, as well as in the present distribution of faunas.

There appears to be an arctic or circum-polar fauna which extends southward to varying distances into the Atlantic and Pacific oceans, permitting certain species to be obtained indifferently off the Alaskan, Labrador, or Scandinavian coasts. Its general southern surface limit is Baffin bay, but it can be traced in deep water into the gulf of St. Lawrence.

A Syrtensian or intermediate fauna extends from northern Greenland downwards along the Labrador shore, on both sides of Newfoundland, in the northern part of the gulf and estuary of the St. Lawrence, and from the Grand bank off the south of Newfoundland westward on all the fishing banks off the Nova Scotia coast to St. George bank and the entrance to the bay of Fundy.

An Acadian or Nova Scotian fauna occupies the southern and western portions of the gulf, generally delimited from the Syrtensian by a line drawn from cape Gaspe outside of the Magdalen islands to the northern point of Cape Breton, but continuing between Anticosti island and Gaspe peninsula where it mingles with the Syrtensian fauna. Southward it is found in the shallower coastal waters on the south of Newfoundland, Cape Breton, and Nova Scotia, as well as in the bay of Fundy (excepting its deepest parts), whence it continues along the New England coast to cape Cod.

The natural bounds of the Virginian fauna are cape Cod and cape Hatteras, but it has outlying colonies in the gulf of St. Lawrence, on the southern shore of Newfoundland, on Sable island and the coasts of Cape Breton and Nova Scotia, as well as to a slighter extent in the more sheltered of the head waters of the bay of Fundy. It is also represented in Casco and Massachusetts bays leading down to its more natural northern limit.

The oyster (*Ostrea virginiana*) belongs to the Virginian fauna, which includes the quahaug (*Venus mercenaria*), the ribbed mussel (*Modiola plicata*), a bar clam (*Mactra lateralis*), a scallop (*Pecten irradians*), and a number of species of smaller Bivalves, such as *Teredo dilatata, Cummingia tellinoides, Montacuta elevata, Petricola pholadiformis, Cytherea convexa,* and perhaps others along the Acadian coasts. To it belong also many Gastropods well known on our coasts such as *Crepidula fornicata, plana* and *convexa, Bittium nigrum,* and *Greenii, Nassa obsoleta, Odostomia bisuturalis, trifida,* and *seminuda, Astyris lunata, Turbonilla interrupta, Utriculus canaliculatus, Bulla solitaria, Buccinum cinereum.* In a similar manner there might be added representatives from other great phyla beside the Mollusca, but of less interest in the present connection. Some of these species are so constantly associated with the oyster that wherever they are found it is understood that the oyster may be looked for, or has perhaps formerly lived there, or at least that the physical conditions are largely suited to its requirements.

The Canadian representatives of the Virginian fauna may have wandered northward during some warmer period such as that which prevailed in Greenland at the time of its discovery by the Norse sea-rovers in the ninth century. The name Greenland given by one of them, Erik the Red, about 980, commemorates the fact of its having once possessed a more genial climate. However this may have been, it is evident that for the last few centuries and at the present time, the oyster and other members of the Virginian fauna are being slowly driven southward by aggression of that Arctic climate which has changed the physical conditions of Greenland.

The explanation of this astonishing climatic change is forthcoming from the facts of geology and physical geography. It has been shown by Gesner, Dawson, Matthew, Hind, Murphy, Chalmers, and others, that the Atlantic sea-board of this continent is undergoing a slow but gradual subsidence, which has amounted in places to as much as eighty feet, while on the other side of the ocean, as is also well known, the coast of Scandinavia and adjacent countries is slowly rising. Such geological changes of level, affecting not only the opposite continents but extending also to the ocean bed, has, according to Verrill, thrown the southwardly flowing cold Arctic Current closer to our shores, while the warm Gulf Stream from the south, due to its outside situation and the configuration of the land, only proceeds as far as to the south of Newfoundland before it is deflected across towards the coast of Norway.

III

DECLINE OF THE OYSTER FISHERY

Statistics.—The catch of oysters in our three Atlantic oyster-producing provinces for the year 1910 was:

OYSTER PRODUCTION IN THE MARITIME PROVINCES FOR 1910

Shipping Stations	Bbls.	Bbls.
NEW BRUNSWICK		14,045
Bathurst	100	
Caraquet	300	
Shippigan	45	
Tracadie	30	
Neguac	2,800	
Bay du Vin	3,800	
Chatham	420	
Richibucto	300	
Buctouche	3,240	
Cocagne	2,200	
Shediac	400	
Botsford	350	
Sackville	60	
NOVA SCOTIA		1,696
Pugwash, Malagash	280	
Wallace River	479	
River Philip	35	
Sterling	5	
West Pictou	90	
Tracadie, Bayfield, Antigonish	201	
West Bay, River Denys, Malagawatch	240	
East Bay, Grand Narrows	10	
Iona, Washabuck, Little Narrows	353	
Baddeck	3	
PRINCE EDWARD ISLAND		11,264
Charlottetown	40	
Point Prim	450	
Pownal	42	
Wheatley River	172	
Crapaud	1,000	
Lot 65	90	
Tracadie	2,050	
New London	50	
Malpeque	927	
Grand River	468	
Bideford	940	
Richmond Bay	350	
Travellers Rest	500	
Wellington	1,000	
Brae	250	
Ellerslie, Lot 12	940	
Carleton	2	
Alberton	1,333	
Other places	660	
TOTAL		27,005

The numbers vary from year to year and sometimes one place drops out of the report or another comes in. This depends upon various conditions, such as the number of fishermen, their success or failure at different places upon trial, their knowledge of former years' results at this or that point, their ideas of testing new regions, whether an area was fished out or not fished at all the previous year, calm or stormy weather, high or low prices, the advantages of other fisheries or occupations at the time.

The statistics of the catch or of the shipments or of the trade from year to year may not be a true statement of the productiveness but they are the only available means of following up the history of the subject. The following condensed table will exhibit the chief events since 1876:

Province	Barrels		
New Brunswick	7,911 (1876)	28,083 (1886)	14,045 (1910)
Nova Scotia	1,040 "	4,318 (1891)	1,696 "
Prince Edward Island	7,905 "	57,042 (1882)	11,264 "

For each province the fluctuating yearly output rapidly rose to a maximum and then slowly declined. The maximum was reached by Prince Edward Island in 6 years, by New Brunswick in 10 years, and by Nova Scotia in 15 years. Roughly speaking New Brunswick and Nova Scotia may be considered to have risen to 4 times, Prince Edward Island to 8 times, and then each to have fallen to less than twice its figures for 1876. The maximum output of Prince Edward Island was reached in 1882, the same year as the maximum (64,646 bbls.) of all three provinces, showing that the island province had control of the oyster trade. In 1900 New Brunswick first surpassed Prince Edward Island in shipments and then fell behind again until 1907, since which time she has taken the lead. In the 35 years between 1876 and 1910 Prince Edward Island turned out 867,226 bbls.; New Brunswick, 554,594; and Nova Scotia, 67,385. In 1871 (the first year for which we have figures) the total output was 39,450 bbls. From this there was a decrease to the minimum of 11,716 in 1875, and then an increase to the maximum of 64,646 in 1882, from which time until 1907, through many fluctuations, and notwithstanding the addition of the British Columbia catch, there has been a general decline to 27,299 in 1907. In 1908 and 1909 there were rises but in 1910 there was a fall. These can not be properly understood at present, but it is probable that the rises were due to strenuous efforts because of high prices, the fall a result of the succeeding scarcity.

The price per barrel rose during the period from \$3 to \$8, and in 1906 the total value of the Canadian oyster trade reached its maximum, although

the catch was only half that of 1882. Many men remember when oysters were only $1 a barrel, while, in recent years, Malpeques have brought as much as $12.

In the early years of the fishery there was a protracted period of indifference, during which the oyster was used by few people and then more as a novelty than as a staple article of food. This was followed by a period of strife between fishermen and farmers as to whether it should be regarded as a food or as a fertilizer. In the meantime improvements in the means and rapidity of transportation had carried oysters inland to a widening market and occasioned a demand which left no room for doubt as to their uses. The at first locally abundant, easily procured, cheap oyster rose in price and became sought after to such an extent that more and more beds were discovered until all our areas had been explored. The demand continued and the natural supply became so far reduced that many people feared all the beds might be depleted and the oyster become a thing of the past. Places that formerly yielded many barrels per year can now furnish none. Beds which were at one time prolific are now not worth fishing. In some districts the greater part of the season's catch is taken on the first day. It is no uncommon spectacle to see fleets of boats assembled over promising areas awaiting the hour of open fishing. I have myself had hauled in succession four dredgefuls of dead shells among which could not be found a single living oyster; and this was on the Shediac reserve, which for seventeen years had been under the care of an oyster expert, but had been thrown open immediately before the election of the previous autumn and almost destroyed by the crowds of fishermen who flocked from every direction and unreasonable distances. The fishing lasted for eight working days, during which time were taken 585 bushels of oysters (and 4,054 bushels of quahaugs), of which 419 bushels of oysters (and 2,853 bushels of quahaugs) were taken on the first day by 91 men. In Bedeque bay, P.E.I., the oyster has apparently been exterminated. Many places along the southern shore of Nova Scotia have become depleted. On the south-western coast of the gulf of Maine, where at one time there were great numbers, there are now perhaps no living oysters. The opinions of fishermen, the comparison of the fishery reports, the examination of particular localities, all point in one direction—that our oyster fishery is rapidly declining and that there is danger of its complete loss.

Natural Agents of Destruction.—This is not surprising. It has been the history of other places and of other fisheries. Under the primitive conditions that exist before man's interference, nature settles into a sort of equipoise whereby the losses due to the accidents of life are made good by reproduction. It is an expensive method but it is the only one possible under the mechanical, self-adjusting processes of unassisted nature. The whole number of individuals remains about the same from year to year. To maintain this balance each adult female in her life-time is required to

leave two successors to take the places of herself and a male. But to accomplish this end she is called upon to deposit something like 16,000,000 eggs each year of her adult life. This condition has been brought about by nature and must be accepted as the most economical possible under natural conditions. It goes to show the magnitude of the death-rate during the period between the egg and the adult and at the same time calls attention to the magnitude of the causes which effect such a colossal death-rate. Brooks has stated that "If all the eggs were to live and grow to maturity they would fill up the entire bay in a single season. The fifth generation of descendants from a single female oyster would make more than eight worlds as large as the earth, even if each female laid only one brood of eggs."

The causes that have operated under natural conditions to prevent the oyster from attaining any such undue prominence are observable or self-evident. There are limitations in the kinds and in the amounts of accessible matters, in the ability of the oyster to make use of these matters, and in the climatic, physical, and biological conditions of its environment. Natural forces react with varying effects upon embryonic, larval, spat, or adult stages. It is not the same cause which effects the greatest destruction upon each, and in some cases this depends upon a combination of causes.

The heat of the sun when applied through a layer of water hastens the activities and increases the chances for life, but when it acts directly upon eggs, embryos, or larvæ thrown up on the beach, it dries out and kills them, whereas spats and adults may withstand exposure for a considerable tidal period. Cold, frost and ice act quickly upon the younger stages, but the larger spat and adults are not so vulnerable. A transference of frosty air from a distance may cool the surface water and this will gradually sink, but it is not likely that oysters suffer much as a result because it could only be the free-swimming stages that would come in contact with the surface and they can sink into lower levels when they feel the cold. The transference of cold from the surface to the bottom by convection is a slow process and, besides, must lose effect in sinking through warmer layers. In relation to changes of the temperature of the air or of the contiguous land and rocks, a mass of water, in consequence of its low specific heat, acts as a great protector of life. It is different in those cases where eggs, embryos, larvæ, and young spat are exposed wet to cold and frost, or where adult oysters are subject to the weight and grinding movements of ice on the beaches of tidal waters.

Pure river-water will kill oysters in every stage of their existence. But when mixed with sea-water or alternated by the ebb and flow of the tides it seems to act as a stimulant. A rain storm can have little or no effect upon any stage of the oyster that is already below sea or brackish water but may do great damage to those exposed at low tide. The older ones

can close their shells and live until the return of the sea-water, but eggs, embryos, and larvæ left stranded on the surface, that might live in cloudy weather until the next tide, may be crushed by the falling drops, beaten into the mud, smothered with débris, or drowned in pools of the fresh water.

Tides, tidal currents, current-movements produced by the wind, continuations of river-currents, waves and storms, may carry floating or suspended stages out to sea or throw them upon the beach, or heap sediment, silt, sand, mud, gravel, stones, shells, weeds and drift on to fixed spat and adult stages, crushing or smothering them.

Eggs may go unfertilized, or settle into masses and pollute one another, or sink into mud, or be eaten by animals. Larvæ may swim or be floated on to unsuitable bottom or eaten up. Spat and adults may be covered with drift, eaten, or otherwise injured or destroyed. All stages may suffer from lack of food, the larvæ from lack of cultch. All are preyed upon by larger or smaller carnivorous or omnivorous fishes and crabs. The oyster crab does not occur in our regions. The star-fish and the drill are not plentiful. The boring sponge attacks some of the shells, softening and weakening them as organs of defence. There are parasitic protozoa and worms and associations with other animals as sponges, anemones, hydroids, bryozoa, tube-worms, tunicates, etc., that result in little or no recognizable injury. More formidable troubles arise from old age and disease.

A very great disadvantage in some respects arises from the gregariousness of oysters, which brings them into competition with one another for place and food and causes crowding and interference with normal growth as well as with the processes of feeding and breathing.

To the preceding may be added those changes which take place on a large scale and which have to do with the elevation or subsidence of continents or portions of them to such an extent that the sea falls off from or flows up farther on to the land. Luckily for the oyster such changes are generally of a slow and gradual nature so that, although a fixed animal, its successors are able to move a little in one direction or the other as the case requires. Much more formidable effects are brought about by changes in the circulation of the ocean water, such as the bringing of frigid currents closer to a region of comparatively mild temperature. It has already been pointed out that this is the case with the oyster areas of Canada. They must be regarded as lying near the northern limit of possible occupancy by the oyster. While the lowering of the temperature of the surrounding sea-water by the Arctic or Greenland current is so slight as to cause no immediate concern, yet, when any area from other causes becomes depleted, its chances for restocking in a natural way are poor. The adult oyster could doubtless become accommodated to a considerable lowering of the mean annual temperature, but what tells

in sustaining the race from generation to generation is the mean temperature of the breeding season, which is more likely to be adversely affected.

Man the Oyster's Greatest Foe.—All these causes of destruction have been in operation for century upon century and have been offset by the enormous powers of reproduction of the oyster, of repair to injuries, and of accommodation to changing conditions. Before the advent of man, and at the present time where man does not interfere, the oyster was and is capable of holding its own in the struggle for existence. But where man interferes, with his reasoned methods of fishing and his selfish disregard for the future of the fishery, he disturbs the balance which has obtained between the natural and opposed powers of production and destruction, and in a comparatively few years reduces the productivity of the natural beds to the verge of depletion. The oyster, in its simple, undesigned, mechanical mode of life, hampered by all its specializations and loss of sensory and locomotory organs, cannot evade or defend itself against the persistence and contrivances of man. If the oyster could reason it would regard man as its greatest enemy, for he not only calculatingly takes every specimen that he finds but in various ways destroys others that he cannot see and almost maliciously interferes with the habitats of all stages of the developing young.

In the first place man strikes at the very existence of the oyster in fishing for and removing from the beds the full-grown, mature, breeding individuals and those next in size that should take their places. In doing this he removes spat on the adults, that are too small for use and should be left in the water where they can grow up. At the same time the removal of all these takes away their shells and reduces the amount of natural cultch in the water. The process of fishing cannot help but break down the natural surfaces of the beds, burying living oysters under dead shells or tumbling them into mud. Oyster fishing on the Canadian coast is accomplished with oyster-tongs which somewhat resemble a pair of rakes fastened together like scissors and operated from boats above the beds—two men in a boat taking from 3 to 6 barrels per day.

In a similar manner the fishing for quahaugs interferes with oysters and spat and stirs up mud in the water to settle on to the surfaces of shells, rendering them unsuitable for the attachment of larvæ.

The digging of "mussel-mud" by farmers is in several ways injurious to oysters. A "mud-digger" consists of a framework suspending a huge dipper-like scoop with a bale and a long beam for a handle. The scoop is lowered through a hole cut in the ice and controlled by men at the end of the beam. The power is applied through a chain that passes from the bale over a pulley and is wound around a vertical windlass turned by a horse. The framework may be slid along to fresh places as the old ones become exhausted. The so-called "mussel mud" is composed largely of decaying oyster shells with some mussel, clam, quahaug or other shells

mixed with mud, and is used as a fertilizer for the land. It contains many good shells that might serve as cultch and sometimes living oysters and spat. The bottom is cut into deep trenches into which the edges collapse. There is a great amount of sediment stirred up, and heaps of mud are left to settle when the ice melts.

Winter fishing by means of rakes through holes cut in the ice was formerly very destructive in that the small, unmarketable oysters were left on the ice to perish.

Oyster shells have been used in the building of roads, and at one time oysters were burned for the lime contained in their shells.

In all this man's influence on the oyster has been one of destruction, injury, hindrance, for which he makes no amends. To pursue these practices would mean ultimate extinction.

Solution: Preservation

IV

CONSERVATION AND INCREASE OF PRODUCTION

Restrictive Legislation.—From this brief review of the forces of destruction we must turn to the methods of conservation and of production. In order to preserve the oyster fishery, the legislature has imposed certain restrictions upon the fisherman, limiting the time, place and manner of fishing, the size of oyster to be taken, the damage and obstruction to the beds. Even before Confederation there had been acts passed in the colony of Prince Edward Island to prevent burning of live oysters for lime, and to limit the oyster fishing to the residents of the colony, as well as making provision for the leasing of areas for oyster culture, and the spending of $1,000 a year on the improvement of oyster beds.

In the year following Confederation was passed "An Act for the Regulation of Fishing and Protection of Fisheries," authorizing the expenditure of any sum appropriated by parliament for the formation of oyster beds, the transplanting of oysters, restocking and fixing a close season from June 1st to September 1st. In 1885 the close season was extended to Sept. 15th. In 1891 a portion of Shediac bay was reserved for oyster culture. In 1892, oyster fishing through ice was prohibited. In 1893, the first code of regulations came into operation with regard to fishermen, boats, licenses, close season, prohibiting night fishing, Sunday fishing, and winter fishing, specifying the size of oyster to be taken (2 inches for round and 3 inches for long oysters), requiring that small oysters be returned to the water, though small sizes may be fished for transplanting, prohibiting the use of rakes and forbidding the digging of mussel mud within 200 yards of live oyster beds. In 1894, Tracadie harbour (Antigonish co.) was reserved. In 1904, the close season was extended first to Sept. 22nd, and then from May 21st to Sept. 22nd, and the size limit changed to 3 and 3½ inches. In 1907, the close season was made from April 1st to Sept. 30th, and only tongs and rakes permitted. In 1901, the first regulations were enacted against the quahaug fishery.

The effect of legislation has been to check the rate of decline by reducing waste and injury, and in this manner to prolong and preserve the oyster-fishery. To have maintained the fishery for forty years is something, but it is not enough. A catch that may have satisfied the demand at one time is barely capable of provoking an appetite at the present day. The number of oyster consumers has been increasing with the population and the facilities for shipping, but the number of oysters fished, so far from keeping pace with the number of consumers, has actually diminished.

We have been trying to make the most of what nature supplies us free and unassisted. Under this method the fishery is declining, the oyster is dying out.

To prohibit the catch is to make the oyster of no use; to permit it is adding to the natural processes of destruction and hastening extermination. We must seek for a means to multiply the number of marketable oysters without having to restrict the catch.

Oyster Culture.—The sea is not illimitable, and its products are not inexhaustible. The oyster is not only confined to shallow water near shores, but to limited portions of the shore water. Brought into existence and sustained for ages by natural processes, it is capable only of defence against natural enemies. It cannot withstand the strain of over-fishing by man. On the other hand man can not expect to continually get something for nothing from the sea. He has not been satisfied with the natural productions of the land, but set himself to the destruction of the more useless, and the increased cultivation of the most useful. He must do the same in relation to the sea. It may be a long time before man gains anything like a satisfactory control over the most valuable migratory fishes, but it is very different with the oyster, which has lost all powers of locomotion except for a brief larval period. It would almost seem to have been expressly designed to lead man from the cultivation of the land to that of the sea. The only way in which to materially and unrestrainably increase the numbers of oysters is to expend labour in extending and improving the natural conditions that are known to be necessary or favourable to the existence of the oyster.

In order to intelligently and advantageously expend labour upon the oyster, or upon its environment, it is necessary to know its complete life-history, and to know the natural conditions of its existence for each of its several different modes of life. Until recently there was at one place a great gap in the continuity of our knowledge; but this is now bridged over and we are sure that we know every stage of its development and with considerable detail. This puts us in a position to judge as never before how, when, and where to best render assistance to the oyster.

The assistance, in its nature, as well as in its manner of application, depends especially upon the natural conditions of existence, the modes of propagation and the methods of culture.

The natural conditions of existence are either extrinsic, i.e. outside of the oyster and reacting upon it, or intrinsic, i.e. within the oyster and fitting it to withstand or make use of external forces. Extrinsic conditions are either physical or biological—physical when they refer to the habitat, biological when they refer to competition, food and the like. Intrinsic conditions are either anatomical and physiological or embryological and developmental—anatomical and physiological when they refer to the structure and activity of the oyster, embryological and developmental

when they refer to the egg and pre-larval stages, the larval or free-swimming stages and the spat to adult stages.

The modes of propagation are either natural or artificial—natural when the eggs are regularly spawned into the sea-water and develop in the usual way, subject to the exigencies of life, artificial when the eggs are taken from an oyster and fertilized by sperm taken from another oyster, while the products are kept under the control of man.

The methods of culture of the oyster do not start with the simplest stage—the egg—as is common in the culture of most living things. In the cultivation of plants it is usual to begin with the spore or the seed. In the raising of fish, birds and many other animals it is the rule to commence with the egg. But with the oyster it is the custom to start with spats that are already considerably advanced towards maturity.

Oyster culture, as generally conceived, is about on a par with the transplanting of small fruit-trees, obtained from a nursery, and looking after them until they are full-grown. This is the reason why oyster culture has been known since early in the historic period, although the egg and first stages of development were not discovered until comparatively recent times. It might easily happen that anchors, ropes, stakes or other objects left in the water of oyster regions could receive a deposit of spat and, acting upon the observation of such an occurrence, somebody began to put out things for the purpose of collecting spat (spat-collectors, cultch or stool). As experience accumulated it would become recognized that some objects proved better collectors than others, or were more easily procured and cheaper and also that spat could only be collected in a certain part of the year. In such a manner a practical method could be developed without a knowledge of what was really taking place.

Methods in Foreign Countries.—Oyster culture has existed in Italy from early Roman times. In the gulf of Taranto and lake Lucrino much of the old method is still preserved. Modern methods in Italy, France, England, Holland, Germany, Belgium, Spain and Portugal have been in part derived from it, and in part are adaptations to special conditions of climate, coast, tide, restrictions of governments, temperaments of the people, demands of the trade, scientific research and many other things that have operated to give character to the industry of each country. In their broader and deeper aspects the methods are essentially the same, the difference being more superficial and arising principally in the materials with which the culturists have to work. *Everywhere the methods have to conform to the mode of life of the oyster and its course of development.*

The first thing for the culturist to do is to get possession of little spat oysters or "seed" as they are generally called. The next is to grow them to marketable size. Seed oysters are procured on the natural oyster beds (banks or reefs), or are captured by artificial collectors. In every country the earliest impressions of the people are that the natural stock is inexhaust-

ible, and it is only later when the production becomes diminished and perhaps verges on depletion, that artificial means such as the putting out of cultch and care of the young spat are resorted to. The artificial means themselves depend upon the remnant of natural production. There are still places, like Taranto in Italy, Arcachon in France, and Whitstable in England, that, because of some fortunate, inherent, physical conditions, have resisted all forces of destruction and furnish starting points in both natural and artificial production. Italy, France, England, Holland, Germany, Spain and Portugal have natural oyster beds from which seed-oysters are obtained. In Belgium there is no natural seed and oysters for cultural purposes have to be procured from neighbouring countries. In Spain, Portugal and Germany the seed oysters are taken on natural banks without the use of artificial collectors. In England dead oyster shells are scattered over the bottom for cultch. In France and Holland tiles are similarly used, or are carefully piled in variously arranged heaps that permit free circulation of water. In Italy bundles of branches of the hazel or the gorse are suspended by grass ropes, supported between stakes. In Japan branch-bearing stems of bamboo are stuck in the bottom. They all accomplish the same object in the capture of young spat that soon become large enough to be recognizable, and as seed may be separated and transplanted to where there is plenty of room and food for growth.

As in the mode for procuring spat, so in the manner of treatment afterwards, there are different practices in different countries. In England and Portugal the seed is transplanted to suitable places along the foreshores. In France, Holland and Spain, the spat are protected for the first year in wire cases before being transferred to a tidal beach, park or "claire."

In *Italy* the spat caught on bundles of branches (fascines) may be separated by chopping the branches into shorter lengths, which are stuck in the suspending ropes. In place of transplanting, the ropes may be removed to deeper or shallower water, and those oysters that become free are placed in depending baskets. Thus all processes of culture may be performed at the one place and by the same culturist, who makes use of the full depth or vertical extension of the mass of water, instead of, or as well as, the horizontal or surface extensionof the bottom as is customary in other countries. On account of the warm climate and the small tidal fluctuation, the Italian makes use of deeper water, whereas in other countries it is the shore, especially between low and high-water marks, that is employed. Collecting and growing may be supplemented by fattening and storing side by side in the same park.

In *France* reckless dredging of the natural oyster banks by all comers reduced the industry until the government was forced to take restricting measures. The culture methods are recent, having been originated by Coste about sixty years ago. There is a specialization of the processes,

such that the culturist who rears the oysters for market buys his seed from the spat collector.

The natural banks are of importance chiefly in the production of seed oysters, which may be procured by dredging. But by far the greatest amount of seed is caught on tiles that, because of their size, shape and weight, are well adapted for this purpose. They can be built in layers crossing each other, with the concave side down, so that the water containing larvæ can readily pass among them and the under surfaces remain free from sediment. They are white-washed with a thick layer of lime-and-sand cement, so that when the spat are of sufficient size or begin to crowd one another for space in growing, they can be easily chipped off without destroying the tiles. Attempts have also been made to procure spat by constructing breeding ponds, by hollowing out and walling in portions of salt-marshes, and placing in them great numbers of spawn oysters. The ponds were sometimes provided with flood-gates, so that the water could be drained off at ebb tide for cleansing purposes, and refilled when required at flood tide. In some years considerable success has been achieved, but it could not be depended upon. Thin, flat, wire cases are extensively used in which the young spat may be retained in numbers, protected from their enemies, or raised above the interference of mud and sediment. Muddy bottoms are adapted to cultural uses by spreading sand and gravel over the surface until a crust is formed. Oyster parks, made by enclosing tracts of tide land by planks, or other barriers sufficient to retain shallow water for a few hours, or more expensive stone-walls with flood-gates, furnish areas of suitable warmth and food supply and serve to protect against enemies and shifting sand or mud. Claires, large or small excavations on marsh or meadow lands, containing a few feet of muddy water and banked by earth or sods are employed to fatten, flavour or colour the marketable oysters. The water is changed only every week or two, contains a great amount of sediment, is badly aërated, warm and salty, and is thick with diatoms, one of which (*Amphipleura ostrearia*) communicates a greenness to the oysters feeding upon it. The green oysters of Marennes have long been famous. Growth is forced but there is a high mortality.

Two other processes are employed in France—disgorgement and education. For the first the oysters are placed on a hard bottom in clean water for a few days, in order to permit a discharge of the black muddy contents of the intestine before marketing. For the second they are accustomed to short periods of exposure out of the water, in order to teach them to tighten their shells and retain their fluids during shipment.

In *Holland* the oyster has been the subject of careful study, and oyster culture has since 1870 been very successful. The limited areas, the leasing by auction for a number of years, the active competition, the frugality of the people and other causes, have contributed towards this. The

methods may be said to be modelled after those of France, but with adaptations because of differences in the coast. The culturist, by obtaining comparatively small areas at different parts of the estuary of the Scheldt is able to perform all operations most economically. There are extensive banks at the foot of the dikes, where no dredging has been allowed, that have escaped destruction and furnish seed. Coated tiles are used as collectors, and are removed into deeper water for the winter. Growing and fattening are accomplished in parks, where wire cases are sometimes employed, or on hard bottoms, where shells are also sown in the breeding season.

In *England* the rich natural supply of oysters, almost rivalling that of Italy in historic antiquity, was long regarded as inexhaustible, and the oystermen believed in dredging as frequently as possible.

Scarcity was put down to lack of spatting seasons, which by some were held to occur about three times during a lifetime. The fine natural breeding grounds of the estuary of the Thames could not withstand the continuous dredging, the drain by the large companies and the proximity of the London market. Continental methods of procuring seed oysters on tiles have met with little success, but the cheaper means of spreading shells broadcast is to some extent practiced. Numerous, varied and sometimes costly attempts to artificially raise spat in breeding ponds have generally failed, while the facility with which seed may be obtained from France tends to restrict oyster culture to the processes of growing and fattening. With large companies, such as those of Whitstable and Colchester, the native spat form but a very small part of the whole number of oysters reared. An abundance of seed readily and cheaply procured in France (or elsewhere) is spread thickly over smooth, hard, level bottom in shallow water (one fathom or less) near the shore, where it is freely moved about and cleaned of sediment, weeds and enemies, and in the spring fresh cultch (shells) may be added, but no attempt is made to extend the cultivable grounds by enclosures like those of France or Holland or by wire cases. Concreted pits or cellars are employed to store oysters dredged for the market, but are not used for fattening, flavouring or disgorgement.

In *Belgium* scarcely anything more than fattening is attempted. Oysters are continually brought from France, Holland or England, and, after a month's detention in the claires at Ostend, acquire a flavour which has won a demand for them in England and France, where they were perhaps first obtained, as well as in Germany.

In *Germany* there is a productive oyster area of about fifty miles length along a portion of the North sea lying to the south of Denmark. This is leased to a company subject to inspection and a large amount of governmental control. The object is to preserve the banks and permit

the greatest natural production without risk of experiment in artificial methods.

In the *United States* the oyster industry is enormous. The fishery extends to every state bordering on the Atlantic ocean from Massachusetts to Texas, of which the most important include Maryland, Virginia, New Jersey, New York, Delaware, Connecticut and Massachusetts, or those states in proximity to Chesapeake, Delaware and New York bays. The waters of these regions undoubtedly furnish as favourable natural conditions as are to be found anywhere in the world, and their capacity for production is stupendous. But, being situated in the oldest inhabited portion of the American continent, in proximity to the densest population and largest cities, and near great railway and steamship lines of distribution, they have been subject to constant and incalculable drain. According to Brooks:

"In many states, as in Delaware, a great part of New Jersey, and especially in Rhode Island, the natural beds have been so heavily drawn upon that they long ago ceased to furnish any marketable oysters, and they are now valuable only as a source from which a supply of small oysters can be gathered each year for planting. In the early days of Rhode Island, oysters were found there in greatest abundance, but although dredging was forbidden in 1766, under penalty of ten pounds fine, the natural beds have been so depleted by excessive tonging that they are now of little value, and they supply only a very small part of the seed used in planting."

Methods of oyster culture have originated in the United States independently of those in Europe.

"The oysterman of East river having observed that young oysters fastened in great numbers upon shells which were placed on the beds at the spawning season, started the practice of shelling the beds, in order to increase the supply, and in 1855, or three years before Coste represented to the French Emperor the importance of similar experiments, the state of New York enacted a law to secure to private farmers the fruit of their labor, and a number of persons engaged in the new industry on an extensive scale. The industry has grown steadily from that time and East river is now said by Ingersoll to be the scene of the most painstaking and scientific oyster culture in the United States."

The first kind of culture to be made use of was that of "planting," which has been employed in New Jersey since 1810. Small, young oysters, gathered from crowded natural beds, are taken to fresh places, where they may be regarded as private property, conveniently looked at from time to time, have more room and food and be freer from enemies or other disadvantages. A greater number are likely to live, they grow larger than they would otherwise do, are more regular in shape, and have a finer appearance and flavour. In two years they may become worth ten times the value of the original small oysters. Planters can afford to go long distances and collect or buy their seed or have it shipped from distant parts, while those from whom they buy may make a specialty of collecting and selling seed.

The seed-collector or the planter may soon pass to the next step in the industry and plant shells (or other cultch) for the purpose of obtaining

a greater quantity and in an easier manner. Instead of as at one time using oyster shells for the building of roads, or burning to lime, he will save them for cultch. He soon learns that a greater success results from planting during or near the spawning season, by using perfectly clean shells, by scattering them broadcast, or by spreading them in a tideway. As much as 1000 or 1200 bushels per acre are used. In the autumn of the same season, he dredges, rakes, or tongs up shells from different parts of the area planted, to see if they have succeeded in a good catch of spat. In case they have, he may leave them undisturbed for three or four years, and then take up and send the grown oysters to the market. Instead of this, however, he may dredge over the bed in the second year from planting the cultch, break the bunches apart to prevent crowding and distortion, perhaps redistribute over the same beds or transfer, and if he is anxious for quick returns, may sell part as seed. In the third year he may cull out the largest for sale, leaving the greater mass to be marketed in the fourth year, after which the ground is again prepared for planting fresh shells.

A disadvantage in the use of oyster or other shells as cultch is that each shell may catch more spat than have room to grow, and on account of the thickness and strength of the shell on which they are fastened the spat can not naturally break apart. In some places, as in Connecticut, small gravel of which each piece could give attachment to only one or two spat has been substituted with success. Where the bottom is not hard, as in portions of Long Island sound, sand or gravel has been used to make a crust on the surface of the mud before planting shells.

In the capture of spat all places are not equally fortunate. It is a mistake to suppose there are floating larvæ everywhere in an extensive oyster region. Cultch must be sown in proximity to living oyster beds, or in the way of currents coming from the beds, in order that larvæ may spread to it either by their own swarming or by the movements of the water. Another practice is to distribute sexually mature and breeding oysters (brood oysters, spawners) over artificial beds, to make sure of the presence of fertilized eggs, with their succeeding larvæ and spat, in the midst of the planted shells.

Complex, laborious and expensive methods, such as those of France and Holland, have not been resorted to in the United States. Tiles, claires and the like are too costly in a country possessing such extensive natural facilities, where oysters are cheap and labour dear. Artificial methods have been chiefly directed towards the procuring and raising of seed oysters, and the fattening and flavouring of oysters of poor quality, that would otherwise find no market. Limited experiments have been tried from time to time, in one place or another, with a view to testing this method or that, suggested to the culturist or adopted from foreign countries, but they have never been brought into general use. In 1879,

Winslow experimented with tiles in Tangier sound, meeting with great success. Stems and branches of the white birch stuck in muddy bottoms of the Poquonock river, Connecticut, succeeded in capturing great numbers of spat. Bricks, pottery, scrap tin, chips, bark, brush, straw, pebbles, etc., have been tried, but the only objects that have found general acceptance are shells. These are nearly everywhere obtainable, and in oyster or other shell-fish regions are sometimes so plentiful as to be regarded somewhat of a nuisance, especially by the shuckers and canners. Oyster shells are the most commonly used, and can be obtained often for the trouble of taking them away. In some places scallop, mussel, clam, or silver-shells are used.

In planting new beds the obtaining of seed is an important consideration. Chesapeake bay retains the greatest natural oyster reefs. Long Island sound possesses gravel beaches that prove favourable spots for a set of spat, but there are places where a set rarely occurs. In Connecticut many shell-planters make a specialty of procuring seed. Its value may vary from \$0.10 to \$1.00 per bushel, depending upon the number, size, and regularity of the young oysters it contains, the distorted shapes, old shells, sponges, or rubbish, the locality from which obtained, the enemies that may be carried over, whether it has been culled or left in the rough state as taken from the beds. The larger the seed the more valuable it is regarded, because the more capable of withstanding injury and sooner marketable. The usual size is from 1 to 1½ inches in diameter. Of course, if the seed is assorted and cleaned, the smaller the specimens the greater number there will be to the bushel and the greater gain when they are grown.

Seed from southern plants is stated to be just as hardy as that in the north. Virginia plantings do well in Long Island sound and spawn in the same summer. Each spring small numbers of Chesapeake oysters are set down and fatten earlier in the fall than the natives. In very favourable places yearlings, it is said, will grow up for market in six months or a year, but it generally takes two or three years. In places it takes longer now than formerly—doubtless because of the greater scarcity of food. The larger bring a higher price, so it pays to leave a year or two longer. The important thing is to sow evenly—not in heaps—300 to 600 bushels to the acre; if too thick there may not be sufficient food and they will grow distorted and be poor.

Methods that prove successful at one place may fail at another. In parts of Long Island sound the planting of southern seed is now almost supplanted by shell culture. The shells must be either so placed that floating larvæ from neighbouring beds will pass, or else native or transported spawn oysters be distributed, among them. In the latter case spawners from not too great a distance are most likely to be best. It is said that southern oysters about to spawn taken to Long

Island sound do not spawn and many of them die in the same season. It has been observed that, when put into much warmer or denser water, sperms rapidly die. If oysters are brought from distant parts they should be transferred to places of similar temperature and density and given time to become adapted. Spawn oysters should be put out before the shells intended for the reception of the resulting larvæ, and not scattered too far from one another. The establishment of new beds by the capture of floating larvæ on dead shells is of more importance than the transplanting of seed oysters. The chances are that most of the latter would have lived where they were—even if they did not grow so fast, so large, or so regular. The formation of a new bed by planting cultch saves the lives of multitudes of larvæ that would otherwise have unavoidably perished. It broadens the area of cultivation and increases the number of possible points of attachment. Seed oysters as well as spawners may likewise be used for a similar purpose, but the general if not the sole use to which seed oysters are put is to be raised to full size for the market. The object is more immediate gain, whereas a little foresight might lead to much greater ultimate gain. By planting cultch on adjoining areas much of the reproductive material thrown off by the growing seed oysters might be saved and lay the foundation for a much greater and more durable oyster bed.

Culture in the Broadest Sense.—Oyster culture in the broadest and most complete sense first became possible when Brooks (1879) discovered the method of propagation by artificial fertilization of the eggs of the American oyster. The method was applied by Rice, Winslow, Ryder, Nelson and others, with a view to rearing the larvæ obtained in this manner to adult marketable oysters.

Brooks, from artificially fertilized eggs, raised larvæ 6 days old, i.e. to the straight-hinge stage. The difficulties are to keep such minute, free-swimming animals in a small, enclosed volume of water so as to be able to find them, to effect a change of water without losing the larvæ, to maintain the proper temperature and to supply food.

Rice, by a simple method, succeeded in keeping larvæ alive for 14 days in a tumbler of sea-water. He stood a lamp-chimney in the tumbler and hung a strip of white flannel over the edge of the chimney and of the tumbler so as to drain away the water, while a similar strip brought fresh sea-water from a supply-tank into the tumbler. One of the larvæ about 44 hours after the eggs had been impregnated thrust out a portion of its velum and became attached to a glass slide upon which it had been placed. He inferred that others may have attached themselves to the bottom and sides of the tumbler.

Ryder became especially enthusiastic and carried out numerous experiments with the object of expanding restricted experimental methods into great commercial enterprises. He wrote numerous articles such as

"Rearing oysters from artificially fertilized eggs," "The oyster problem solved," "The oyster problem actually solved," "A new system of oyster culture," "An exposition of the principles of a rational system of oyster culture, together with an account of a new and practical method of obtaining oyster spat on a scale of commercial importance." Ryder's methods were to raise young larvæ by artificial fertilization and to turn them out, either at high tide, or through a canal, which might be either open or provided with a filter, into natural or artificial ponds connected with the sea. He believed that since oyster larvæ diffuse themselves throughout the three dimensions of a body of water, to obtain good catches of spat it would be only necessary to put in their way immense surfaces of cultch. His plan was to insert numerous perforated trays bearing shells, or vertical strainers filled with shells, in the canal leading to the pond, so that the water carrying oyster larvæ would pass among them with the rise and fall of the tides.

Nelson has been at work in New Jersey since 1888 and has made numbers of valuable experiments and observations. To use his own words (1904, p. 420):

"Our ultimate aim is to establish a system of oyster culture that shall be as much under control as is fish culture."

He raised larvæ from artificially fertilized eggs and tried to keep them in tumblers, tanks, boats, claires, pockets of different kinds of cloth, dialyzers of paper, etc., until they would set as spat. The first part of the process—the raising of larvæ to young shelled stages—has been very encouraging, but the last part—the obtaining of spat—has met with little or no success.

It might be going too far to say that failure was always due to the same cause, but there was a cause common to all these cases sufficient to account for the failure. Rice, Winslow, Ryder and Nelson, all worked under the mistaken belief that the larvæ, when still in the straight-hinge stage and about two to five days old, settle down and affix themselves to become spat. This mistake arose from chance observations of young artificially-reared larvæ temporarily or abnormally clinging by velum or mantle.

In 1901, Nelson wrote:

"The fry, after about five days, develop a two-valved shell and then they seek a place to settle down on."

He did not free himself from this view until 1907:

"It is usually stated that the developing oyster swims around in the water about a week, or less, before it sets on cultch. Last year we were inclined to believe that the interval of free life was less than two days and we felt that this view was not only corroborated by our own observations, but also by those of Colonel Macdonald, the lamented brilliant chief of the United States Fish Commission. Our studies this year seem to emphatically negative such views........ In this stage, called the protoconch stage, there is steady growth for at least a week, and possibly three weeks.......... The actual size of the larval shell at times of setting is one-fiftieth of an inch in length."

In 1908 he again proposed the question:

"What is the length of the free-swimming life of the oyster fry?............The answer was left in a state of uncertainty, so we were anxious to decisively solve this problem during the present year, and we accordingly made it the primary quest of our experiments.......... We found the length of time which elapses between spawning and spatting to depend somewhat on the temperature of the water. At a temperature ranging between 70 and 75 degrees Fahrenheit, the fry required about three weeks to mature to the spatting stage. At a temperature ranging from 75 to 80 degrees the period is only two weeks."

In the same year he began to distinguish "small," "medium," and "large" larvæ, and stated that:

"When it is ready to set as spat it has grown more than sixty fold in bulk, and attained nearly a hundredth of an inch in length."

It will be clear that Nelson's views varied from year to year, and that such statements as those made in 1901 (p. 322): "The bottom and sides of several of the tumblers were covered with spat in the first shell stage," and 1902 (p. 336): "We occasionally secured a complete development of the fry up to the spat stage," were mistakes of the same nature as those of Rice and Ryder. These were not true fixations but accidental or abnormal temporary attachments of straight-hinge stages. Nelson's first correct understanding of the full-grown larva dates from 1907, when he made numerous, laborious filtrations of sea-water and examined the residue with a microscope.

V

PROPOSED IMPROVED METHOD OF CULTURE

Application of New Knowledge.—In 1904, at Malpeque, P.E.I., during my first summer's work on the development of the oyster, I made discoveries which throw new light on the possibilities and methods of oyster culture. Up to that time the earliest stages of development were known only from the egg to the young, artificially reared, straight-hinged, shell-bearing larva of nearly twice the diameter of the egg, and representing a period of growth of six days or less, depending upon the temperature. At this stage artificially raised larvæ, from want of food or lack of fresh sea-water, die off. The next stage known was the youngest natural spat of at least four times the length of this young conchiferous larva and, as we now know, from three weeks to one month old, reckoning from the time of fertilization. There was a period of two to three weeks in the development of the oyster that was not known—the appearance and organization, the exact time of the year, the place of occurrence, the length of the period and the mode of living, were all unknown. These I determined.

For a period of three weeks, more or less, according to the temperature of the water, the individuality of the larva, the food supply and other conditions, the young oyster swims about in the water, creeps or rests on the bottom, feeds, grows and develops its organs. During this period it increases to something like one hundred times its cubic contents at the beginning of the period, and becomes correspondingly heavy, strong, more capable and more active.

The things of importance from the standpoint of oyster culture are to know when, where and how to procure, recognize and observe the larvæ during this period, because it is the period immediately preceding spatting, and if we can keep track of their progress throughout this interval we can determine the best time to put out cultch.

The larvæ, as we have seen, may be procured by towing a plankton net behind a boat above or in the region of oyster beds during July and August. Oyster larvæ constitute only a small part of the catch and it is necessary to be able to distinguish them. It is possible by examining collections every day or two to follow up the growth of the larvæ to the time when they cease their active swimming life and settle on to shells, stones, stakes, or other natural or artificial cultch and become attached as spat or are lost. Throughout this swarming period the larvæ are few; at the beginning small, at the end large. For the greater

part of the time there is a mixture of all sizes, but a certain size may be most abundant, as if constituting a distinct brood. There may be two or three different distinct broods. Knowing the life-history and the approximate period of growth it is possible to judge approximately when any one brood will reach the stage of full-grown larvæ ready to spat. For greater assurance they may be followed from day to day right up to the limit of larval growth. This is the time to put out cultch for that brood. Cultch put out a few days before or a few days after may catch some spat belonging either to that brood or to others, but it cannot catch so many.

Necessity of Clean Cultch.—It is well known that cultch to be successful in the catching of spat must be fresh and clean. After it has been in the water for a time it becomes coated with slime, organisms and sediment, to such an extent that the oyster larvæ can find few or no spots upon which they are able to fix themselves. Oyster shells form the most readily accessible and very best cultch, but when put into the water they become coated and largely lose their efficiency in even a few days. Hence the necessity of holding the laboriously prepared, good, clean, white oyster shells until a proper time arrives for planting them. If they are placed at a wrong time and do not secure a set of spat, they have to be again taken up and spread out to dry and bleach in the sun, which kills the organisms and allows the slime and sediment to dry, crumble and fall off in handling. There is not only the loss in time and labour in re-cleansing the cultch, but there is the much greater loss of the opportunity to secure the best catch of spat—perhaps a complete loss for the season.

Observation of success or failure over a long period of time has narrowed down the practice of oyster culturists to certain situations, methods and dates. The situations are natural oyster regions or such as can be made oyster-producing. Of the methods, the procuring and planting of natural seed and the management of cultch, are the most important. The date for planting cultch, so far as is practised on the eastern coast of the United States, is the latter part of June or first half of July. Sometimes planters strike a fortunate time, sometimes not. Even if they count themselves lucky the chances are that they have been only partially successful. The catch may be so small as to be scarcely worth the trouble. There may be a complete failure to obtain seed . It has been stated that in some years there has been no set of spat.

Winslow in 1884 wrote:

> "Thousands of dollars would be annually saved by the Connecticut oystermen if they could determine, with any approximate accuracy the date when the attachment of the young oyster would occur. Hundreds of thousands would be saved if they had any reliable method of determining the probabilities of the season."

Determination of Time for Planting.—This is now possible. The practices of oystermen are rules gained by experience and more or less

blindly followed. They are of advantage, but they lack intelligent adjustment to the locality and the season. Since temperature plays so important a part in the growth and reproduction of oysters, and since the temperature varies with localities and seasons, is is impossible to fix on a date that is equally good for all places and all years. To be quite correct the date should be decided for each locality and for every year. An expert, instructed and qualified in the method of taking plankton and in identifying and following up the progress of the oyster larvæ, can tell almost to a day when, for any situation and for any season, is going to be or is the best time to put out cultch so as to secure the greatest set of spat. A general yearly date, such as the last week of June or the first week of July, may be sufficiently close to meet with some success or be useful as a time for which to have preparations made, but the best results can only be reached by taking into account all the accessible information relative to the special occasion, and combining the two most important factors of the maximum number of full-grown larvæ on the one hand and an abundance of good fresh cultch on the other. It might even be advisable, under some circumstances, to divide and distribute the cultch in such a way as to accommodate different broods of larvæ, or to meet weather conditions.

This method does not start with eggs, like the artificial and restricted experimental method of the few zoölogists who can raise up young oysters to the early conchiferous stage of the larva, but, from the inability to supply suitable food, aëration and temperature, are incapable of carrying them beyond that point. Some day it may be possible to cultivate diatoms side by side with the oyster larvæ they are to nourish, and then perhaps the larvæ may be artificially grown to the spatting stage. Neither does the method start with spat oysters of considerable size, purchased as seed or collected at favourable points, like the historic method of oyster culture in England, France, Holland, the United States and other countries. It takes account of both methods and begins between them, just in time to avoid the mishaps of the former and to strengthen the one weak point in the latter, viz., the difficulty of procuring spat. It allows the developing young to pursue their natural course as long as there is no overwhelmingly destructive condition to be met. It takes advantage of the colossal number of larvæ lavishly provided by nature to offset the exigencies and accidents of life and ensure a reasonable chance of keeping up the stock. It places in their way the conditions best fitted for their requirements. I believe that all the artificially fertilized eggs that could be turned out into the sea would not materially alter the number of successful spat. Of the countless millions of oyster larvæ in the water about oyster beds, but relatively few find suitable natural places for fixation. Numerical comparisons of the umbo-stages of oyster larvæ in the plankton and of the young spat that follow in the same regions prove that this is

at least one point in the life-history of the oyster at which the greatest destruction takes place. This is also one point at which it is in the power of man to render assistance. The suggested manner of doing it is not new, but the method of determining the exact time to do it, is new, and that is the all important thing. Hitherto we have had no reliable method of calculating the right time. The time of spawning, even if it were practicable for it to be carefully judged by extensive and accurate examination by a competent zoölogist, is too remote from the critical point of spatting to be of great service. The observation of spat already deposited comes too late for application. The taking and examining of plankton is the only practicable and reliable method of becoming informed as to whether it is worth while putting out cultch at all and, if so, at what time it should be done. For the two seasons with which I am acquainted at Malpeque the proper time did not arrive until nearly the middle of August. It may require considerable patience and assurance to quietly hold cultch until this time of the year, but it is exactly this assurance which the facts of observation substantiate. The facts are so plain and reasonable as to almost remove the process of spat-catching from the region of doubt, caprice and chance, to that of expectancy, regularity and certainty. It makes oyster culture as sure as farming.

It may be that in the United States the time for planting cultch is earlier than in Canada; that in more southern latitudes there is not such a definite approach to a periodicity in spawning, swarming and spatting; that in some places an oyster can develop and deposit spawn a second time in the same season. These and other questions need re-examining. The prevalent, mistaken belief in a very short larval period, and the practice of gauging cultch-planting by the doubtfully determined time of spawning, a month before spatting takes place, can not but have led to many kinds of errors. When all such subjects are again examined by capable men, with improved methods, I feel sure that both theory and practice will be put on a much surer footing.

The researches of Brooks and his co-workers put American away ahead of European knowledge of the oyster, but still left unknown the natural life of the larva. The larval life of the oyster and of its associates among bivalve molluscs was the last obscure chapter in the general history of development of these animals and in the data for a comparative embryology. This was due to the lack of application of plankton methods in the study of the larval periods of marine animals. The systematic employment of plankton methods in the discovery of bivalve larvæ in their natural habitat, combined with parallel faunistic studies of the same regions, have now made it possible to clear up this obscurity in the life-history of the oyster, and to apply the knowledge gained as an important addition to the practical methods in use for oyster culture.

Rendering Assistance to the Oyster.—As a general method it may be proposed, in brief, to observe the natural conditions of existence—both extrinsic and intrinsic—of the oyster and of each different stage of its development. Distinguish the useful from the detrimental. Increase and improve the former, decrease and remove the latter.

Assistance may be given (1) directly to the oyster or its developing young, (2) indirectly through improvement of the environment.

It is conceivably possible to:

1. Increase the number of fertilized eggs by
    - (1) planting spawning oysters near enough together to effect natural fertilization,
    - (2) artificially fertilizing oyster eggs and turning out some stage of the product into suitable places.
2. Save eggs and larvæ by improving the environment to prevent
    - (1) smothering in mud,
    - (2) carrying away by currents,
    - (3) being eaten up by other animals.
3. Create facilities for spatting by planting cultch at the proper time and place.
4. Care for spat by
    - (1) guarding against sediment, crowding, enemies, frost, storms, etc.,
    - (2) furnishing food.
5. Turn to use suitable unoccupied areas.

Coastal regions may be classified into

1. Suitable natural oyster areas.
2. Adaptable areas.
3. Impossible areas.

Food is always present, although in variable kind and amount, everywhere along the coast. Rock, gravel, sand, clay, mud, ooze, etc., may be found without going very great distances. Salinity in any degree between that of the saltest sea-water and the purest fresh water may be found by moving either out towards the ocean or in towards gulfs, bays, coves, estuaries, rivers, creeks, etc. The temperature, the condition of greatest importance, must for some part of the summer season rise to certain degrees of warmth and maintain them for sufficient time to permit the breeding processes. The conditions on an oyster bed must be very favourable so far as the requirements for fertilization are concerned, for there are myriads of both eggs and sperms within reach of each other. Artificial fertilization destroys the adult oysters used and turns into the sea such small numbers compared with what are already there as to be negligible. Differently constituted stages of the developing oyster may

be best adapted to different sets of conditions, yet in nature all the stages are confined to the situation in which the parent oysters are placed. The culturist can move oysters to more favourable places or change the conditions in which they are found. Transplanting oysters from one region to another does not add to the total number of oysters. But, if left to breed instead of being taken up for sale, it will eventually increase the numbers by offering greater advantages in space and food and diminishing competition.

The best outlook in the whole field appears to be to increase the set of spat. To this end, extend old beds and prepare new ones. Place spawn oysters on the new beds. Have ready an abundance of good cultch. By the method described, determine the time for maximum spatting, and plant cultch to suit the occasion. Leave undisturbed for a few weeks or months, as the case may require, to let the young spat grow. When large enough, separate and transplant to where there is plenty of room and an abundance of food. Remove sediment, weeds and enemies.

To accomplish this, *oyster fishermen must become oyster farmers.* They cannot expect to troop to the natural oyster beds and continue to carry away a bounteous harvest without assisting in its production.

Hitherto there has been no inducement for fishermen to expend labour upon the beds, because others would join in the fishing and reap the benefit of their labour. Now culturists are able to obtain leases to water areas, to have these areas surveyed and protected as private property. Leaseholders ought to be exempt from close season and other restrictions. Areas not leased may be regarded as public property and subject to the same regulations as at present.

With this encouragement many fishermen and farmers may be induced to take up oyster culture as an industry, and devote their labour and their earnings to the improvement of oyster beds, the increase of production, the benefit of the trade, and the supply of a wholesome food.

To facilitate, encourage and warrant these undertakings the Dominion and Provincial governments have come to an agreement whereby the Federal authority recognizes the right of the Provinces to grant leases, though still retaining the right to regulate the fishery. This puts an end to that conflict of jurisdiction which so long exerted a depressing effect upon the industry.

Education of Fishermen.—In addition, the Government might originate a campaign of education of fishermen, farmers, culturists, overseers, traders, shippers, or others concerned, with regard to the importance of the new departure and the best methods to be employed. The instruction could be imparted in two ways: (1) through demonstrations, and (2) through suitable printed literature. The demonstrations could be somewhat after the type of our government agricultural, experimental and model farms, and could exhibit the important stages in the development

of an oyster, as well as at the same time show how to conduct the essential operations of oyster culture. For this purpose the Shediac reserve and perhaps another in Richmond bay could be fitted up as demonstration oyster farms and be used also as experimental stations to continue the investigation of oyster questions, to test the application of new suggestions and to reduce cultural knowledge to a system. In this connection I may quote a statement by Winslow in 1884: "I know by experience that the fishermen cannot be reached by anything written or said; they can only be taught by what I may call 'object lessons.'..................

"The value of model and experimental stations is attested by the great influence such establishments had in assisting the French oyster-culturists in their efforts to re-stock the oyster beds of the French coast. In 1858, there was a very great scarcity of oysters, and in consequence the Imperial Government undertook the re-stocking of the beds and the establishment of oyster farms. To-day the waters of France are again prolific....." It might be added that when once the fishermen have seen and handled the objects, and have seen the methods applied and taken part in the operations, they are then, and not until then, in a position to understand and make use of suitable printed literature on the subject.

VI

TRANSPLANTING ATLANTIC OYSTERS TO THE PACIFIC

Incidental Removals.—In connection with the subject of oyster culture, it may be stated that oysters have many a time been carried outside of the present limits of their distribution, but apparently without establishing colonies. The practice of taking them aboard schooners and steamers bound for more or less distant ports cannot have failed to make opportunities for settlement in foreign parts. I have found or dredged oyster shells at many places in the vicinity of St. Andrews, N.B., Canso, N.S., and Gaspe, Que. Every autumn a schooner (or more) is awaited in Montreal with its cargo of Caraquets. On several occasions such vessels have been forced by the unexpected early arrival of winter to seek shelter in Gaspe bay where, after satisfying the local appetite, the bulk of the oysters was thrown overboard. That there are no living oysters in the bay was abundantly shown by my own very thorough dredging and plankton operations extending over two summers there. Gaspe is no very great distance from Caraquet and it is conceivably possible for larvæ to drift that far, yet even the north shore of the Chaleur bay (across from Caraquet) appears to be devoid of oysters. It would be an interesting, instructive, and perhaps useful experiment to put out, under the most approved conditions, suitable quantities of good seed or brood oysters in a few selected places to the north and south of our present oyster region, and have them guarded and examined for a few years. An experiment started in 1902 to determine whether oysters can be cultivated in Annapolis basin, N.S., an arm of the bay of Fundy, has, as far as I can judge, not been looked after with much care, and leaves the most important points either unobserved or only guessed at. There is no doubt that within the bounds of our present oyster regions there are many places where planting and cultivation could be successfully carried on. These should be seeded with our best grade of oysters, rather than with cheaper varieties from the United States that may also transport parasites or other undesirable enemies.

Transplantation from East to West.—Transplantings of small quantities of Prince Edward Island oysters to British Columbia were made under directions of officers of the Dominion Government in 1896 and again in 1905. Last summer (1911) I had an opportunity of examining some of the survivors of the latter year's plant and found them growing and breeding, which proves their ability to adapt themselves, and suggests the advisability of making further and more extensive transplantations along

suitable parts of the coasts of our maritime provinces, on both the Atlantic and the Pacific oceans. A suggestion may be made that the shipment, and especially the planting, should be in the hands of somebody acquainted with the physical requirements of the oyster. There is no use going to the trouble and expense of transferring either young or brood oysters to such a distance to be finally dumped into mud, or left exposed to sun and frost, or even to picnickers and Indians. The situations should be carefully and not too hurriedly selected beforehand, and no foolish concessions made to the selfish desires of local petty politicians. As an example of the manner in which Government jobs sometimes fall into the hands of incompetent or careless persons, I may mention a former shipment of lobsters to the Pacific, which were, I am told, turned out without first removing the wooden plugs that had been placed in their great claws to prevent them fighting and injuring one another during transit.

In the United States, oysters have from time to time been taken from the East to the West but, as in Canada, so far as I can learn, never with any very intelligently planned method of planting permanent and productive colonies. It may have been fancied that the small numbers scattered here or there might some day occasion a startling discovery of an enormous propagation. But it is safer to judge that the larger shipments were put out with a view to the local trade. In 1869 three carloads of eastern oysters were sent to San Francisco, and after over-stocking the market, the rest were planted in the bay, where, it was said, they lived and thrived. In later years it was stated that there had been no success in breeding, and it has been very generally believed that, while Atlantic oysters may live, they will not breed in Pacific waters.

According to Townsend (1891): "The oyster industry of the Pacific coast, exclusive of the trade in the small indigenous species, has never extended beyond the limits of the bay of San Francisco, where it has been restricted to the growing or fattening of seed or yearling oysters, brought annually in large quantities from the Atlantic coast and kept in the waters of the bay until they attain a marketable size."

In November, 1884, seventeen barrels of Canadian oysters were taken to Europe, and, after a journey of almost twenty days, they were planted in the Little Belt, only about 5 per cent of them having died. Their subsequent history does not appear to have been followed.

A Baseless Belief.—Being aware of the lack of reliable information with regard to the oyster's ability to accommodate itself to new conditions, especially so far away from its native home, and finding myself last summer (1911) at the Dominion Biological Station in Departure bay near Nanaimo, B.C., within reach of three of the small bays in which Atlantic oysters had been deposited in 1905, I made strenuous efforts, under very unfavourable circumstances, to obtain some satisfactory observations. The prevailing opinion, among those entitled to

an opinion on such a subject, was that the oysters had all died, or if by chance there were any left, it was certain that they did not breed. My first efforts were to determine if the eastern oyster can live from year to year in western waters. If so, it can ripen its reproductive cells and spawn, and then fertilization and development can take place. There was no information to hand as to what portions of the bays the oysters had been distributed in. I had to make use of research methods to discover what should have been recorded.

Hammond bay, the most accessible of the localities, is small, and I could easily over-run all the beach at a low tide. On the left, after entering and passing well up towards the disused whaling station, I found many half-shells of Prince Edward Island oysters, disposed within short distances from what appeared to be the centre at which they had been deposited. I dredged outwards from this spot to see if there were any living oysters in the deeper water but could not find any. Later in the season I found a couple, stuck in the mud, near the centre of distribution, still living.

Nanoose bay, some twelve miles distant, and perhaps five miles long by a mile and a half broad, was a much more difficult case, for five barrels of oysters might have been thrown out on to a small area of the beach, or of the extensive flats, or below low-water mark. Upon my first visit the tides were neap and unsatisfactory, so I tried dredging and was afterwards surprised to find that I had actually judged to within a few rods of the place. The second visit was devoted to a more complete survey of the bounds, depth and bottom of the bay. On the third visit, which was planned to strike a low tide, I went almost directly to the spot and soon discovered some shells which led me to the centre of distribution. This was far up past the mountain and the little cove on the right and in the first swale outwards from Webster's north-east corner post. There were a good number of living Malpeques still remaining, some of them with bits of Prince Edward Island red-sandstone attached. Compared with my recollection of the small oysters about Ram and Curtain islands in Richmond bay these appeared to have grown considerably. They varied from two and three quarters to five inches in length, the original size of the planted oysters being marked off from the new growth by a deep or broad furrow. I took sixteen selected living specimens home for careful examination and found that only one had already spawned (July 17), while the other fifteen were ripe and generally distended with eggs or sperm. At 7.10 p.m. of the same day I put together eggs and sperm in a tumbler of sea-water and at 7 a.m. next morning there was an abundance of segmenting stages and swimming larvæ. These observations proved that Atlantic oysters can be transplanted to the Pacific and remain healthy and grow; that they can come to maturity and ripen their reproductive

cells; that they can spawn, and that the eggs develop into active free-swimming young.

Plankton taken on every occasion at Hammond and Nanoose bays had not yielded any oyster larvæ, which became explainable upon making the preceding observations of the reproductive organs. It was still a little too early in the season. On the 25th I obtained a second lot from Nanoose bay of which the forty-seventh was the first to yield eggs, all the previous ones having spawned with the exception of four or five containing sperms. The interval between the two visits had been the hottest of the summer and the oysters had nearly all spawned in this period—slightly later than is usual in the Atlantic.

On the 27th I made a trip to Ladysmith (Oyster harbour) about fifteen miles from the station, where I had good fortune in finding a trace of the few remaining transplanted oysters. These are near to Mr. Page's house. I examined several individuals and took plankton, which for the first time contained larvæ of the Atlantic species. They were recognizable by their familiar shape and proportions, but did not present such a deep pink or brown colour as in the native home of the Prince Edward Island oyster. A selected specimen with characteristic postero-dorsal high umbos, large convex left valve and small flatter right valve, velum, foot, pigment-spot, etc., measured (Oc. V, obj. 4) 42 long by 37 high (=.289 x .255 mm.)

The only remaining bit of evidence desirable to prove that the Atlantic oyster can breed successfully in the Pacific, and that its brood can grow up into healthy oysters, would be to find stages of its spat from the smallest possible up to the size of the transplanted eastern oysters. It was of course too early for the present year's spat, and I did not have much time to look for those of a previous year. This was the sixth summer from the date of the transplanting and some of the oysters may have been mature four or five years. The amount and character of the new growth of shell (on one of two specimens could be made out six additions in growth) suggested that it may have taken some time for them to become acclimatized or accommodated to the new conditions, so that it is not likely that any of their progeny had attained to a size larger than the accompanying native Pacific oysters. It is reasonable to suppose that the comparatively few descendants of the two and a half barrels planted in Hammond bay, five barrels in Nanoose bay, and one barrel in Oyster harbour, when dispersed over the broad areas at their disposal, and reduced by the usual combinations of circumstances, and especially in the presence of thousands of British Columbia oysters of varying sizes, shapes, and complexions, would not prove at all conspicuous objects. It is likely that young spats of the two species are not easily distinguishable from the exterior. Without this information, the facts of maturity, spawning, fertilization, embryonic and larval development, previously referred to, are conclusive.

Falling in line with these observations it may be stated that other Atlantic animals have been transferred to the Pacific and found conditions sufficiently similar to become colonized. The Atlantic clam (*Mya arenaria* L.) has propagated enormously, notwithstanding that it has more competitors than in its original home. Atlantic lobsters (there are no native lobsters on the Pacific coast) have been turned out in the region, and are claimed by some to be still living, and, it is suggested, may be breeding, although I have heard of no evidence. On the contrary it has been declared, again without evidence, that the water is not sufficiently saline for the lobster. In the 1896 Report of the Marine and Fisheries Department, p. 291, it is stated:

"At New Westminster we transferred the whole shipment to the tug provided. We steamed over 100 miles from five o'clock in the morning till nine at night but could not find the water sufficiently salt anywhere............ The rest we put overboard in deeper water en route to Nanaimo, hoping the water would be more salt near the bottom............"

In "Marine Life," Vancouver, of February 1909, an article on "The Acclimatization of the Lobster" takes those concerned to task for having no better reason than "hoping the water would be more salt near the bottom." In an important undertaking like this there should certainly have been preparation made beforehand in determining the best situations, depth, temperature and salinity, since it was necessary upon arrival to get the lobsters into suitable water with all haste. But the author of the criticism was equally unfortunate in his methods, since, although having been stationed in the locality for years, he was not in possession of such data.

Temperature and Salinity of Pacific Waters.—As temperature and salinity are important considerations when contemplating the transplantation of oysters, lobsters, or other desirable food animals, I shall give a few data selected from a long list of observations taken from the first day of my arrival until the day before leaving.

Date 1911	Place	Temperature Cent.	Temperature Fahr.	Salinity (distilled water =1.000)
May 16	Entrance to Departure bay (near Biological Station)...............	14°	57·2°	1·020
" 20	Half way to Nanaimo,...	12·5°	54·5°	1·020
June 10	Station................	16°	60·8°	1·0185
" 20	Hammond bay.........	17°	62·6°	1·0165
July 1	Station (shallow water, low tide).............	21°	69·8°	1·018
" 14	Nanoose bay...........	18°	64·4°	1·0185
" 22	Gulf of Georgia.........	17·5°	63·5°	1·022
" 28	Station (shallow water, low tide)..............	24°	75·2°	1·0167
Aug. 7	Off Hammond bay......	17°	62·6°	1·019

Comparison with readings on the Atlantic coast (see page 92) will show that lobsters as well as oysters may be confidently expected to thrive in the Pacific if put out with proper care. In Richmond bay, P.E.I., the great centre for the oyster, there are several lobster factories. Everybody connected with fishery pursuits should know that in a body of sea-water of a few fathoms depth the bottom has a greater salinity than the surface, which, along with its lower temperature, is an advantage to the lobster to a greater extent than to the oyster, the former preferring off-shore areas, but the latter keeping near land. Both Atlantic and Pacific oysters are brackish-water species to a much greater extent than the European species.

Government action in transplanting Prince Edward Island seed and brood oysters to suitable selected areas of the British Columbia coast, under trustworthy surveillance, would doubtless go a long way towards settling our most reputable variety of shell-fish in those regions, and towards the preparation for a greater productivity of marine food for the future inhabitants of the province. The greatest and most rapid results would be reached by private enterprise, because of the greater attention and protection received by the oysters. In Nanoose bay, judging from the new posts put down to mark the limits of prospective planting areas by Webster, Wallis, and others, there are already indications of a desire to enter into private oyster culture.

VII

THE BRITISH COLUMBIAN OYSTER

(*Ostrea lurida*, Carpenter)

Description.—Before making any headway in the study of the transplanted Prince Edward Island oysters I had begun to gather information on the occurrence, distribution, size, shape, colour, structure, breeding, etc., of the native British Columbian species. This oyster had been noticed in a faunistic way by Carpenter (Suppl. Rep. Brit. Assoc. 1863, p. 645), Dawson, Whiteaves, Newcombe, Taylor, and others, and more closely with regard to its mode of breeding by Prince (Peculiarities in the Breeding of Oysters, Special Reports 1895, Ottawa). It occurs from Queen Charlotte sound south-ward along the coasts and coastal waters of British Columbia, Washington, Oregon, and California. In the gulf of California occur a large species (*Ostrea iridescens*) and one (*Ostrea palumea*) or two small species, all of which have received little attention.

In Departure bay the British Columbian oyster is not common, but a few small specimens may be found under stones exposed about one hour above low-water mark in front of the Canadian Pacific Railway cable house, and usually so broadly and solidly attached (with the left valve against the under side of the stone, i.e., uppermost in the natural position) that it is scarcely possible to separate them without destroying the attached valve. A few occur under like conditions just inwards from the far point at Hammond bay. On the extensive flats exposed at low tide at the upper ends of Nanoose bay and Oyster harbour they occur by thousands, free on the surface, and more or less spotted with barnacles.

Good specimens reach two inches in length by an inch and a half in breadth, with a straight dorsal and a semi-circular ventral margin. The right, upper, or smaller valve is nearly flat or but little convex, and fits into the margin of the left, lower, larger, and very convex valve, the greater part of the ventral and posterior margin being scalloped, while the left valve may be fluted and knobbed, presenting an appearance very much resembling small oysters of the short or rounder variety at Ram island, Malpeque. The colour is usually dark (those under stones lighter) with the older parts weathered grayish, and the umbonal region of the left valve is often attached to a small stone or another oyster or bears a scar. Internally the shell is extensively pigmented, dark with small bands or blotches of lighter pearl, while the muscle scar is rather lighter and banded. The mantle is broadly margined with dark, which may also creep up on to the abdomen.

In size, colour, and flavour, the Pacific oyster is much inferior to the Atlantic species, but in places (e.g. Oyster harbour) it is extensively collected by the Indians, and may be seen on the markets of Vancouver and other cities.

Hermaphrodite Character.—A most interesting and important feature of the Pacific oyster is its divergence in some respects from the mode of breeding of the Atlantic species, and its resemblance in the same respects to the common European species (*Ostrea edulis* L.). *This is a most fortunate circumstance, since it prevents any possibility of cross-fertilization and inter-breeding between Atlantic and Pacific species,* and permits our most estimable Prince Edward Island oysters to be planted in British Columbian waters without a chance of hybridization reacting to lower their standard of superiority. In our western species their is no primary separation into males and females—each oyster is like every other one, or, as it is also stated, the sexes are united in each individual; otherwise expressed, each individual is bisexual, hermaphrodite, or monœcious. Our eastern species is exactly the reverse, being diœcious or unisexual, i.e., every individual is either a male or a female.

My first observations were made on July 12th, on specimens procured under stones near the Biological Station. Nearly all appeared to be males and, as they were of small size, I took it that, as commonly occurs, the males had ripened first. But one was of medium size and contained eggs, that at once attracted my attention on account of their large size and opacity—the nucleus being rarely observable. Measured exactly as all my former measurements they were: Oc. V, obj. 2=6.5; Oc. V. obj. 4=15; Oc. V. obj. 7=72. Another individual procured a day or two later, with an abundance of eggs, pure and ripe, oozing from the oviduct, gave the almost unvarying measurement of Oc. V. obj. 7=75, which, when calculated, is 75 x 1.45=108.75μ=slightly over .1 mm.=slightly over 1/250 inch,=fully twice the diameter of the egg of the Atlantic oyster, and perhaps identical with that of the English or common European oyster.

Upon turning to the spermatozoa I found them in every individual —even between the eggs of those containing eggs in the gonad. The younger individuals had no ova but all sperms. Some of the older ones had a few big, soft, opaque, irregular, elliptical, oval or nearly spherical eggs, scattered among irregular masses of less than half their size, which are balls of spermatids on the way to becoming spermatozoa. One of these measured 46 x 40 μ and each one is kept in a dancing or rolling movement, somewhat like that of many infusoria, by the flapping of the tails of the ripening spermatozoa on the surface. Between these masses are millions of free, mature, swimming or moving spermatozoa, of which the tails are rarely visible until they are looked for under a high power. I have not made extensive measurements of the spermatozoa of

this species, but I believe they are smaller than those of the Atlantic oyster, which may have some relation to the particular mode of fertilization, such as being introduced by the respiratory current, for fertilization must take place in the mantle cavity. In some parts of the gonad ova may be plentiful, while at other places there are only sperm-balls. Later, in the warmer weather, the sperm may be pretty well run off and the reproductive organ contain mostly eggs. In this way the younger oysters, and the older oysters at the beginning of the season, may be physiologically males, while older oysters at the height of the breeding season may be physiologically females.

Specimens from Hammond bay showed the same phenomena. After finding an abundance of the larger and more normally occurring oysters at Nanoose bay, I decided to make a more extensive examination to determine if there were more than one species, or if the first found specimens under stones were the same as those exposed on the surface of gravel, sand, or mud flats, and I brought home a pail-full of picked specimens to keep as a convenient stock from which to select and study at leisure. In making measurements it is important to use only ripe eggs, that are freed from each other and flow easily, and to select those that are spherical or nearly so and not flattened by the weight of the coverslip, as well as to extend the measurement to many oysters in order to exclude all possibility of mistakes. On July 16 one of the specimens contained about half a tea-spoonful of eggs in various stages of segmentation, lying free in the lower valve—a mass of white granules. Ripe eggs ooze from the oviduct into the branchial cavity, between the two folds of the mantle, where they are retained next to the gills and without any retaining, sticky matrix. It must be here that they first meet with ripe sperms from other individuals, for before this the sperms of the same individual have been ripened and discharged. At this time the whole oyster appears exhausted—the gills rent, the flesh collapsed, emaciated, soft and discoloured, as if undergoing decomposition. On July 24, I opened one hundred of the stock supply, and found only six with eggs, embryos, or conchiferous young in the branchial cavity. All the others were in process of spermatogenesis and oögenesis.

Artificial Fertilization.—An experiment that has often suggested itself to me is to do the same with the common European oyster by way of artificial fertilization as Brooks did with the Atlantic oyster of America. Now that I had a species essentially the same as the European, I tried it, and apparently with success. I separated out a mass of ripe eggs from the body of one individual, and a mass of motile sperms from another, and mixed the two masses. There developed embryos from the mixture. Of course it is difficult to be sure that sperms had not already had access to some of the riper eggs, while in the oviduct. Unripe eggs are of no use; eggs freed from the gonad and lying in the mantle cavity are very likely

to have come in contact with sperms already—those that are in process of segmentation are sure to have done so. This restricts the experiment to finding specimens just before, but just on the point of, extruding eggs.

I also tried Atlantic oyster eggs with Pacific oyster sperms, as well as Atlantic oyster sperms with Pacific oyster eggs, but without success, as might be expected.

Comparison of Species.—I mounted eggs, embryos, and larvæ of both species together under the same coverslip for comparison—those of the small British Columbian oyster looking like giants beside the corresponding stages of the large Prince Edward Island oyster.

For the study of segmentation the Atlantic oyster is of advantage on account of the smaller size and greater transparency of the eggs. The order of segmentation in the Pacific species appear to be the same as that of the Atlantic, and to be subject to similar variations. I have found in the mantle cavities of parent British Columbian oysters all stages from the egg up to those stages in which their own minute shells were as large as .138 mm. in length. I have taken larvæ in the plankton of which the shells were as small as .165 mm., as well as different larger sizes. The young must leave the protection of the parent somewhere between these two sizes. They have a straight hinge-line of half the length of the shell, and are of a general light complexion, with five or six dark blotches in the regions of the liver and the velum.

Some of the preceding statements come into conflict with what Prince wrote in 1895. His paper states:

> "Under specially advantageous circumstances I have been enabled to carry on investigations upon three distinct species of oyster, each distinguished by peculiarities in breeding habits which are of the highest moment."

These were the English, the Eastern Canadian, and the British Columbian oysters. His original contributions refer to the last:

> "The two elements (eggs and sperms) are found in different individuals in our Atlantic oyster. In other words the male oyster is distinct from the female. The same holds true for the British Columbia oyster, as my researches last summer on the Pacific coast demonstrated for the first time.............. The eggs were less than one-third the diameter of the English mollusc................ The number of males was greatly in excess of the females."

The eggs examined must have been immature—taken from the ovary. The great excess of males was doubtless due to the time at which they were examined, but no mention of date or particular locality is made. Reference is made to Hoek's observation that a European oyster containing eggs in the reproductive ducts was found to contain sperms two weeks later, and was therefore female at one stage and male at another. The statement that:

> "All investigators agree that nothing of this kind has been discovered in Atlantic oysters,"

would not hold for the present day. Kellogg (1890) states:

"The European oyster, *Ostrea edulis,* is hermaphrodite, but in the American form, *O virginana,* the sexes are separate. While rearing the young of this form from the eggs of Woods Holl, with Mr. Harrison of the Johns Hopkins University, we found a specimen apparently containing both eggs and spermatozoa. On sectioning parts of the generative gland, I found it to be hermaphrodite, as was suspected........late in June, near the end of the breeding season."

Prince further states:

"In my investigations upon the Pacific coast in the Dominion cruiser 'Quadra,' I captured many small embryo oysters several miles from any known oyster areas."

This is possible—they may have been carried by currents, instead of wandering by their own swimming powers. But on the other hand there is no proof that they were oyster larvæ. At that time the larva of the oyster had not been distinguished from those of the commonest bivalves associated with the oyster, not to mention the scores of others. There is no mention of place, date, how taken, or how recognized to be oyster larvæ. If the author had first learned to recognize those in the water by comparison with those in the pallial cavity of the parent he would have discovered that, like the English oyster, but unlike the eastern American species, the British Columbian oyster guards its young for a time, and maybe this would have led him to observe also that it is hermaphrodite.

Moore (1897) writes:

"According to Professor Schiedt, a hermaphrodite oyster occurs on our northwest coast, the specimens examined coming from the state of Washington, the exact locality not being mentioned. Sexually therefore, this species resembles the common oyster of Europe."

VIII

SUMMARY OF OBSERVATIONS AND DISCOVERIES

The discoveries, observations, advances, generalizations, or applications of most importance made in the course of this work are:

1. The first systematic application of the plankton net in the search for and obtaining of oyster larvæ.
2. The first recognition of the older stages of the larva of the oyster.
3. Oyster larvæ can be found in the water about oyster beds.
4. They are almost confined to the months of July and August.
5. They may be taken at the surface and at various depths below the surface.
6. All stages from the freshly fertilized egg to the full-grown larva are suspended in the water or lying on the bottom.
7. The stages hitherto unknown, constituting the "blank" referred to by Jackson, that could not be raised from eggs by artificial fertilization and culture, are most conspicuous in the plankton, and it was due to lack of plankton study that they had remained unobserved.
8. The free-swimming period is considerable—close on a month—not one or even six days as had been thought.
9. The larvæ swim suspended in the water, or sink and rest at the bottom, feed, and grow from a length of ·062 mm. to a length of ·386 mm.
10. During this time they pass through a shell-less, a straight-hinge, and an umbo stage.
11. The larval shell (prodissoconch) is asymmetrical, as is also to some extent the contained body.
12. A probable explanation of the asymmetry is given.
13. Ctenidial axes and lower filaments of inner hemibranchs are present in the older larvæ.
14. Pigment spots (eye-spots) are present.
15. The otocysts contain otoconia.
16. A foot, homologous with that of Molluscs in general, is present in the older larva (simultaneously with the velum).
17. A byssus gland is present.
18. Cerebral, pedal, and visceral ganglia are present.
19. In locomotory organs, nervous system, and sense organs, the full-grown larva has a higher organization than the adult oyster.
20. The first recognition of the very young stages of Canadian spat.
21. Spat are found attached to shells, stones, etc.

22. They occur first in August.

23. Normal fixation takes place when the shell of the larva has reached a length of about ·38 mm. and is in the umbo stage, not, as was formerly thought, in the smaller and younger straight-hinge stage.

24. A probable explanation of the method of fixation is given.

25. A metamorphosis occurs immediately after fixation through loss of larval organs, as velum, foot, eye-spots, otocysts, cerebral and pedal ganglia, etc., and a development of permanent organs, as spat-shell (dissoconch), outer hemibranchs, palps, etc.

26. The age of the chief stages has been determined approximately by fixing the time of the chief events, as spawning, swimming of the trochophore, appearance of straight-hinge shell, umbo stage, spatting, sexual maturity.

27. An accurate system of measurements has been introduced, and a comparison of actual sizes at different changes of habit or of structure.

28. Size is a more useful criterion than age, since organization advances with growth in size, which depends more upon temperature and food than upon age.

29. Sections of both larvæ and spat have been prepared and studied.

30. Important organs, as the intestine, gills, etc., have been followed through both larvæ and spat.

31. Development has been traced to adult sizes.

32. Cross-fertilization between two of the most divergent varieties (Malpeque and Caraquet) was accomplished.

33. Free-swimming larval, creeping, or fixed stages of the commonest accompanying allied bivalves have been identified and distinguished from those of the oyster.

34. The physical conditions of oyster beds in different situations have been compared.

35. The temperature and other conditions for breeding have been determined.

36. The time of spawning has been narrowed down to a more definite part of the year and to a briefer period than was formerly thought.

37. The free-swimming period has been limited to the month of the year, and the duration of the time.

38. The time of spatting has likewise been determined as to month and duration.

39. The importance of the larva and of the larval period has been recognized.

40. Since the free-swimming larva precedes the fixed spat, then a systematic microscopic examination of plankton collections may be employed practically to determine when, for any area and for any year, the masses of larvæ will first reach maximum size and be ready to become fixed as spat, i.e., when is the best time to put out cultch.

41. The preceding particulars of structure, habits, development, times, places, periods, foods, temperature, salinity, etc., make progress in oyster culture seem possible.

42. An improved method in oyster culture is proposed.

43. Prince Edward Island oysters transplanted to British Columbian waters live, grow and breed, and the eggs, embryos, and larvæ develop.

44. They could be transplanted to many places up and down our Atlantic coast, with a likelihood of living if looked after.

45. Native British Columbian oysters resemble the English (common European) oyster, and differ from the Atlantic oyster of this continent.

46. The eggs do not pass out at once into the sea but are held for a period in the pallial chamber, where development through the embryo and into the straight-hinged shell stage of the larva takes place.

47. Experiments in cross-fertilization between British Columbian and Prince Edward Island oysters give no results.

48. Since interbreeding between them is impossible, they may be raised on the same beds without lowering the standard of either.

49. The hermaphrodite condition of the British Columbian and common European oyster is doubtless most primitive, and the diœcious state of our Atlantic oyster and of the Portuguese oyster is secondary or most specialized.

50. Numerous structural, developmental, physical, or other observations have been made, that are of interest from a zoölogical point of view or of use from a cultural standpoint.

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